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Toru Nakamori

ABSTRACT

Ecological features such as diversity and coverage of the Recent hermatypic corals in Ishigaki-jima and Sesoko-jima in the Ryukyu Islands are measured by a transect method. Communities, growth form and zonation of the corals are discussed on the basis of the measurements. Fifty-one coral genera and 144 species are recorded in this study and 11 hermatypic coral communities are recognized on the basis of the ratio of species. Six topographic areas are discriminated in the coral reefs in these two islands. Each community is distributed in the specific topographic area, but the same community does not necessarily appear in the same topographic area of different reefs. On the other hand, the distributions of the dominant growth forms of corals within a reef are fairly constant not only in the Ryukyu Islands but also in the Indo-Pacific Region.

Relationships between the diversity and coverage of the hermatypic corals apparently show the ecological succession and support the intermediate disturbance hypothesis (Connell, 1978).

The growth forms of *Porites australiensis* indicate eco-morphological variations. They are spherical, hemispherical and laminar at depths of 0, 10 and 30 m respectively. The growth rate of the corallum of *P. australiensis* decreases exponentially with depth. The increasing rate of corallum surface area is constant, having no relation to water depth. A model for corallum eco-morphology of *P. australiensis* is proposed in relation to light intensity.

Stratigraphy of the Ryukyu Group is investigated in Hateruma-jima, Miyako-jima, Okinawa, Okierabu-jima and Kikai-jima. The strata in these islands are correlated with one another on the basis of radiometric ages and nannoplankton biostratigraphy. Ecological studies of fossil hermatypic corals are carried out on five formations of almost the same age; the Takanasaki Formation (Hateruma-jima), Miyako-jima Limestone (Miyako-jima), Naha Formation (Okinawa), Okierabu-jima Formation (Okierabu-jima) and Takigawa Formation (Kikai-jima). The rate of fossil corals to the total rock volume is determined for each taxonomic and morphological group. Fifty-two genera and 70 species are identified. Five fossil communities (Communities A-E) are recognized on the basis of measurments, which can be correlated to the Recent ones. The number of genera decreases and equitability increases with increasing latitude. The rate of fossil corals to the total rock volume also decreases with latitude.

Depositional environments of six facies of the Ryukyu Group (coral limestone, rhodolith limestone, detrital limestone, *Cycloclypeus-Operculina* limestone, calcareous sandstone and conglomerate) are inferred by utilizing paleontological and sedimentological information. Paleogeography of the five islands are reconstructed based on the distributions of the coral communities and the depositional environment of the facies.

Key Words: hermatypic coral, reef, Ryukyu Islands, community, coverage, diversity, zonation, Ryukyu Group, stratigraphy, paleogeography

CONTENTS

INTRODUCTION

Many ecological studies on coral reefs until the 1960's were concentrated on the qualitative descriptions or the quantitative studies on the shallow places in the reef (Stoddart, 1969). As summarized by Sheppard (1982), after the development of SCUBA equipment, quantitative studies using quadrat or transect methods have been carried out on the reef slopes in Discovery Bay, Jamaica (Goreau, 1959; Goreau and Goreau, 1973; Lang, 1974), Curaçao, Netherlands Antilles (Bak, 1975; Van den Hoek *et al.*, 1978), Eilat, Gulf of Aqaba (Loya and Slobodkin, 1971; Loya, 1972), Aldabra Atoll (Barnes *et al.*, 1971), Tuléar, Madagascar (Pichon, 1971, 1978), Réunion Island (Bouchon, 1981), Chagos Islands (Sheppard, 1980, 1981), Great Barrier Reef (Veron, 1978; Veron and Done, 1979: Veron and Hudson, 1978; Wallace and Lovell, 1977), Fanning Atoll (Maragos, 1974) and Hawaii Islands (Dollar, 1982; Grigg, 1983). In these studies, ecological properties such as diversity, coverage and zonation of reef corals were reported and the mechanisms of these structures were discussed. To understand the dynamics of coral communities, the ecological succession has been given attention in the recent studies (Grigg and Maragos, 1974; Crame, 1980, 1981; Grigg, 1983).

In Japan, hermatypic corals are distributed along the Kuroshio Current from Hateruma-jima, situated at latitude 24° 04′N in the Ryukyu Islands, to Boso Peninsula (35°00′N) on the Pacific side and the Noto Peninsula (37°30′N) on the Japan Sea side. They occur also in the Izu and Bonin Islands. In these areas, typical coral reefs, which are mostly fringing reefs and aggregations of patch reefs (Hori, 1977), are formed between Hateruma-jima in the south and Kotakara-jima in the north (29°15′N).

Yabe and Sugiyama (1932, 1935 and 1941), Yabe, Sugiyama and Eguchi (1936) and Sugiyama (1937) recorded 37 genera and 124 species of the hermatypic corals from the Ryukyu Islands. Recently, more than 69 genera and 231 species, containing the hydrozoan coral *Millepora* spp. and octocoral species such as *Heliopora coerulea* and *Tubipora* *musica*, were reported in the same region (Nakasone *et al.*, 1974 ; Eguchi, 1975 ; Hirata, 1975 ; Horikoshi, 1979 ; Yamazato *et al.*, 1982 ; Yaeyama Branch of Okinawa Pref. Fisheries Exp. St., 1983). The richness of genera is equal to that of Micronesian reefs or Maldive Islands which have been thought to be the generic center of hermatypic corals in Indo-Pacific Region (Wells, 1954 ; Rosen, 1971).

The species composition of shallow communities in the Ryukyu Islands were described in some reefs (Hirata, 1975 ; Horikoshi, 1979). Yamazato (1971) and Yamazato *et al.* (1967) divided qualitatively the reef slope coral communities through the Ryukyu Islands into several groups and discussed the zonation structure. Quantitative spot descriptions of coral communities using the quadrat method were made in Kume-jima and Senkaku Islands (Yamazato *et al.*, 1980 ; Yamazato *et al.*, 1982). Coral communities and their zonation in Ishigaki-jima were studied by the transect method in the vast reef areas from the moat to the reef slope (Takahashi and Koba, 1977, 1978 ; Takahashi *et al.*, 1983 ; Takahashi *et al.*, 1984 ; Takahashi *et al.*, in press). These investigations made clear the species compositions of some coral communities and their zonations in the Ryukyu Islands.

However, ecological studies on the hermatypic corals in the Ryukyu Islands are still insufficient for correlation of ecological structures to those of other coral reefs and for elucidation of mechanisms of coral community structures.

On the other hand, little attention has been paid to paleoecological studies of the fossil corals from the Pleistocene Ryukyu Group. The Ryukyu Group consists of limestones, sandstones and conglomerates, and occurs in most islands from Taiwan to Takara-jima. It contains numerous fossil corals and retains the ancient reef structures.

The first purpose of the present study is to describe vertical distributions of the Recent hermatypic corals and their community structures in the Ryukyu Islands, and to discuss the generalized zonation pattern. In order to investigate the distribution of those corals, I surveyed Recent coral reefs at four stations in Ishigaki-jima and Sesoko-jima.

The second purpose of this study is to clarify the community structures of Pleistocene fossil corals in relation to those of the Recent ones. The fossil corals were investigated in the correlative strata of the Ryukyu Group developed in five islands of the Ryukyu Islands.

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Table 1. Location of island and physical factors.

	Hateruma-jima	Ishigaki-jima	Miyako-jima	Naha (Okinawa)	Yomitan (Okinawa)	Okierabu-jima	Naze (Amami-oshima)	Kikai-jima
Longitude Latitude	123° 47'E 24° 03'N	124° 10'E 24° 20'N	125° 17'E 24° 27'N	127° 41'E 26° 14'N	127° 44'E 26° 26'N	128° 42'E 27° 26'N	129° 30'E 28° 23'N	129° 56'E 28° 18'N
Annual Mean Temperature		23.8°C	23.1°C	22.4°C		22.3°C	21.3°C	
Annual Mean Temperature of Surface Water		26.0°C		24.8°C			24.4°C	
Mean Maximal Temperature of Surface Water		30.1°C		28.5°C			28.6°C	
Mean Minmal Temperature of Surface Water		22.5°C		21.6°C			20.8°C	
Global Solar Radiation (MJ/m^2)		16.4		13.7			11.4	

Iryu for his kind presentation of data about Recent sediments and stratigraphy of the Ryukyu Group.

Thanks are due to Mr. Shohei Otomo of the Institute of Geology and Paleontology, Tohoku University for photographing the corals and to Mr. Teruo Ishikawa and Mr. Masaaki Shishido of the same Institute for preparation of thin sections.

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I. Recent Corals

1. Description of Study Area

(1) Localities

The localities used in the study are shown in Fig. 1 and Table 1.

To obtain the ecological data, I surveyed the Recent coral reefs at three localities (St. 1, St. 2 and St. 3) in Ishigaki-jima and one locality (St. 4) in Sesoko-jima, close to Okinawa (Figs. 2 and 3). The stations 1-3 were chosen, because the coral genera and species

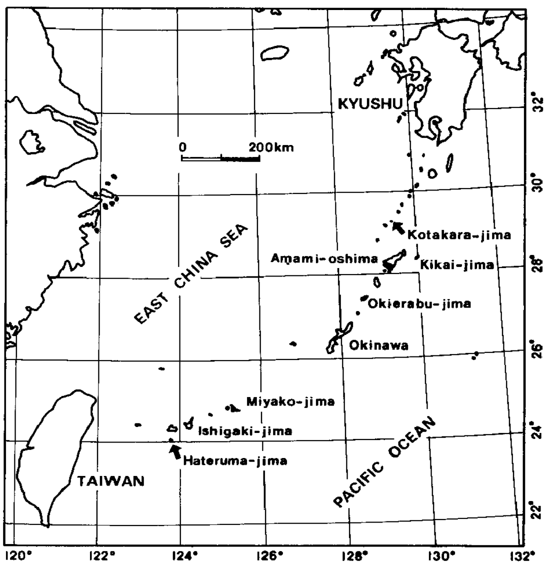


Fig. 1. Map showing locations of the study area.

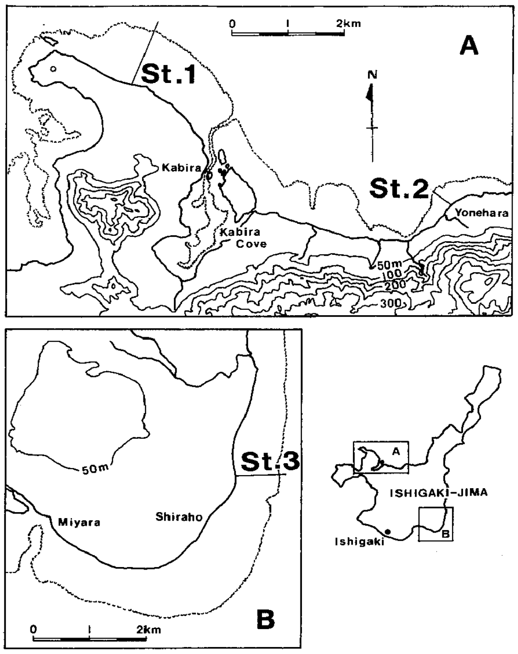


Fig. 2. Location map of St. 1, St. 2 and St. 3 in Ishigaki-jima. Lines drawn at each station indicate fundamental lines.

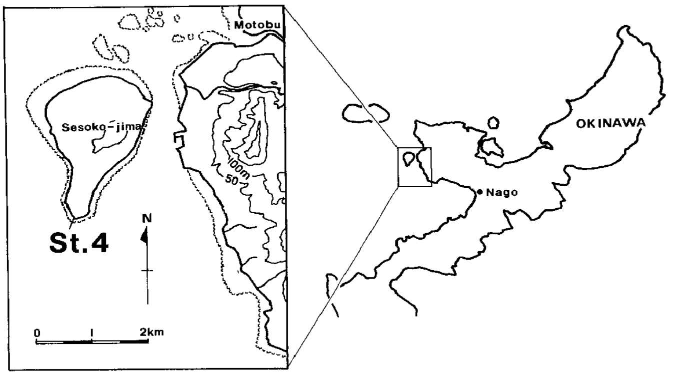


Fig. 3. Location map of St. 4 in Okinawa. Line at St. 4 indicates a fundamental line.

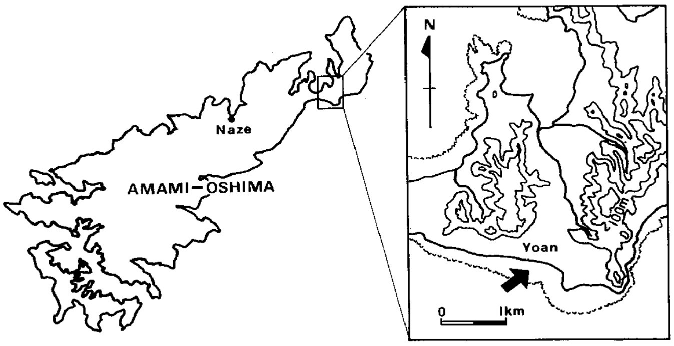


Fig. 4. Location map of sample localities in Amami-oshima.

hitherto reported are the most abundant in Ishigaki-jima among the Ryukyu Islands (Eguchi, 1975; Yaeyama Br. Okinawa Pref. Fish. Exp. St., 1983), and because typical fringing reefs can be seen around this island. Station 3 is located at opposite side of St. 1, and the difference of ecological features of both stations was examined. The fringing reef in Sesoko-jima (St. 4) was also chosen for the purpose of comparison among the reefs here studied. Colonies of *Porites australiensis* were collected from St. 1, St. 4 and Yoan, Amami-oshima (Fig. 4) to measure the growth rate of coralla in three regions which represent geographically southern, middle and northern parts of the Ryukyu Islands, respectively.

(2) Climate

Annual mean temperatures at Ishigaki, Miyako, Naha, Okierabu and Naze are cited from the Climatic Table of Japan, Part 2, Monthly Normals by Stations published by the Japan Meteorological Agency, Tokyo. They vary from 23.8°C in Ishigaki to 21.3°C in Naze, Amami-oshima (Table 1). These values indicate that the Ryukyu Islands belong to the subtropical regions. According to JODC (Japan Oceanographic Data Center), annual mean temperature of surface water is 26.0°C off Ishigaki-jima and 24.4°C off Amami-oshima. The difference between mean maximal and minimal temperature is about 8°C throughout the Ryukyus (Table 1). Mean minimal water temperature off Amami-oshima (20.8°C) is almost at the limit for the growth of hermatypic corals (Wells, 1954). Table 2 indicates the vertical distributions of water temperature of the region off Ishigaki-jima, Okinawa and

Amami-oshima. These values were calculated from the data published by JODC. In each region, the highest values are obtained from 0 to 10 m in depth and the difference of the temperature between 0 m and 50 m depths is only about 1°C, which is smaller than the latitudinal difference of the surface water temperatures within the Ryukyu Islands.

Global solar radiations in Ishigaki, Naha and Naze were referred from the Climatic Table, Part 2 published by the Japan Meteorological Agency, Tokyo. They decrease parallel with increase of the latitude (Table 1), but this phenomenon does not indicate latitudinal decrease of radiation energy from the sun, but instead is due to local variations of cloud density. If the percentage of sunshine was 100%, the global solar radiations would be the same within the Ryukyu Islands.

Distribution of wind directions was reported in Kabira Ishigaki-jima by Yaeyama Br. Okinawa Pref. Fish. Exp. St. (1983), and in Sesoko by Nishihira (1974). According to them, N to NNE wind prevails from winter to spring and S to SSW wind in summer. These bimodal distributions of wind directions were observed throughout the Ryukyu Islands ; because of this reason, Ryukyu coral reefs do not show characteristic features of windward or leeward sides.

The Kuroshio Current, which is known to be the typical warm current, runs through the Ryukyu Islands from southwest to northeast ; this makes the water temperature much higher than in the other regions of the same latitude.

(3) Geography and Geology

The reefs at Kabira (St. 1) and Shiraho (St. 3) are of fringing types and have the clear moat-crest systems whose width is about one kilometer, while the reef at Yonehara (St. 2) has a narrower reef flat (250 meters) and a lower reef crest than those of St. 1 and St. 3 (Fig. 2). The moat-crest system cannot be observed at St. 4 in Sesoko-jima, and the outer reef flat adjoins the coast directly. The Kabira Cove whose deepest part is about 15 m in depth, connects with the open sea by a narrow pass. Small reefs and coral patches distribute along the coast. In Amami-oshima, the fringing reef with moat-crest system of 500 m width is also developed along the Yoan coast.

Some terraces consisting of the Ryukyu Group develop in Ishigaki-jima and there is no big river which disturbs the development of coral reefs near St. 1, St. 2 and St. 3. Behind St. 4, a terrace consisting of the Ryukyu Group stretches along the coast. In Yoan, the basement of the Recent reefs is Cretaceous sandstone and slate (Osozawa *et al*., 1983). The Pleistocene and Holocene sediments around Yoan are poorly developed.

2. Methods

In order to examine the vertical distribution of environmental physical features, I measured water temperature at the moat and the reef slope ranging from 0 to 30 m in depth at St. 1, St. 4 and Yoan. Intervals between measuring points are 5 m in depth. The measurements were performed in August, 1982 and May, 1983 at St. 1, in June and September, 1983 at St. 4 and in September, 1983 at Yoan. Illumination intensities were also recorded on the reef slope at St. 1 and St. 4. RIGO-Submarine Illuminometer Type 2501-A was used for determination. Data from St. 1 were obtained at 11 : 00 on 21st. May, 1983, when the cloud amount was 0.7. Data at St. 4 were measured at 14 : 00 on 1st. September, 1983, when the cloud amount was 0.0.

For the ecological analysis, I adopted the line transect method used by Loya and Slobodkin (1971), Loya (1972) and Porter (1972). At each station, a fundamental line was provided perpendicularly to the coast line. Transects with a length of 10 m were prepared, parallel to the coast along the fundamental line. The intervals of the transects are 25 or 50 m in horizontal distance in the reef flat, while they are 5 m in depth in the reef slope. The lengths of transects which encountered coral colonies were recorded with their specific name in the field. The colonies which could not be identified in the field were sampled for taxonomic study in the laboratory. Representative specimens of each species were also collected. Water depth, substratum type, water temperature and illumination intensity were recorded. In the depth of 30 m on the reef slope of St. 1, quantitative measurements could not be carried out because of technical restrictions. Therefore, only qualitative observation was made in the depth.

The profile of the coral reef at each station was made and divided into several topographical areas. Species diversities and coverage rate of each species were calculated for every transect.

For the growth form and growth rate analyses, colonies belonging to the genus *Porites* found in St. 1, St. 4 and Yoan area were collected from the moat to 30 m in depth. In the laboratory, vertical slices 5 mm in thickness were cut out from the colonies along the growth axis following the method described by Knutson *et al.* (1972) and Buddemeier *et al.* (1974). X-ray exposures were made using Softex Type CMR. Fuji Softex Film HS was used, and exposure KVP values ranged from 30 to 40 KV depending on specimen thickness.

The annual growth rate of corallum and annual increasing rate of surface area of corallum were measured from the soft x-radiographs. The annual growth rate of corallum was represented by the width of a pair of density bands at the top of every colony. The annual

Table 2. Vertical distributions of annual mean water temperature off Ishigaki-jima, Okinawa and Amami-oshima.

	Ishigaki-jima	Okinawa	Amami-oshima
0m	26.0°C	24.8°C	24.4°C
-10m	26.0°C	24.9°C	24.4°C
-20m	25.8°C	24.7°C	24.3°C
-30m	25.7°C	24.5°C	24.2°C
-50m	25.1°C	23.8°C	23.6°C

Table 3. Vertical distributions of water temperature at Stations 1, 4 and Yoan.

	Kabira(St.1)		Sesoko(St.4)			Yoan
	Aug.	May	Jun.	Jul.*	Sep	Sep.
moat	32.1					32.0
0m	30.8	25.5	26.7	27.7	29.8	29.8
-10m	29.2	24.2	26.8	26.7	29.4	
-20m	28.6	23.1	26.8	26.8	28.3	
-30m		23.0	26.4	26.6	28.3	28.4
-50m				23.6		(°C)

* Nishihira(1974)

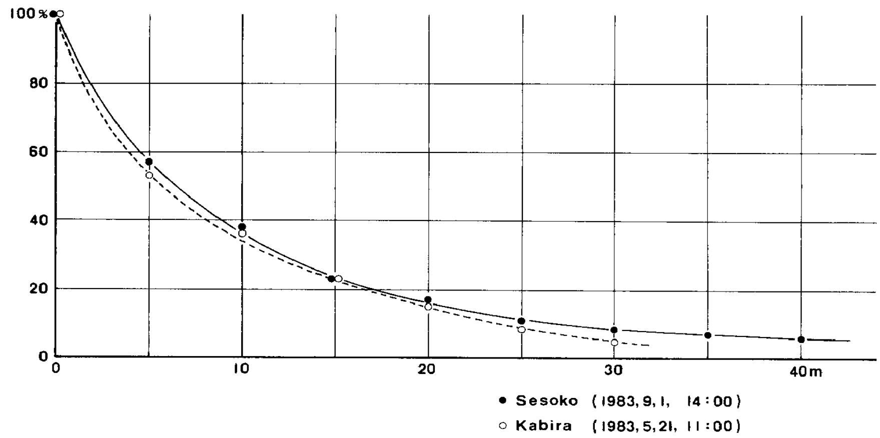


Fig. 5 Illumination intensity at St. 1 (○) and St. 4 (●). Horizontal axis indicates depth (m) and vertical axis relative illumination intensity to intensity in surface water (%).

increasing rate of surface area was calculated as the annual increasing rate of the length of living part of corallum in the x-radiograph.

3. Results

(1) Water Temperature and Illumination Intensity

The vertical distributions of water temperature just on the reef slopes and the moats at St. 1, St. 4 and Yoan are presented in Table 3. Compared to the vertical distribution of water temperature off each station (Table 2), it is characteristic that the differences between 0 and 30 m in depth are generally bigger than those of the offshore. Reference data at St. 4 (Nishihira, 1974) were added in Table 3. Nishihira (*op. cit.*) mentioned that there is a thermal discontinuity layer between 30 and 50 meters in depth. In summer, the water temperature on the moat often exceeds 32°C, but seldom reaches the degree at which hermatypic corals can not survive.

Figure 5 indicates the relative illumi-

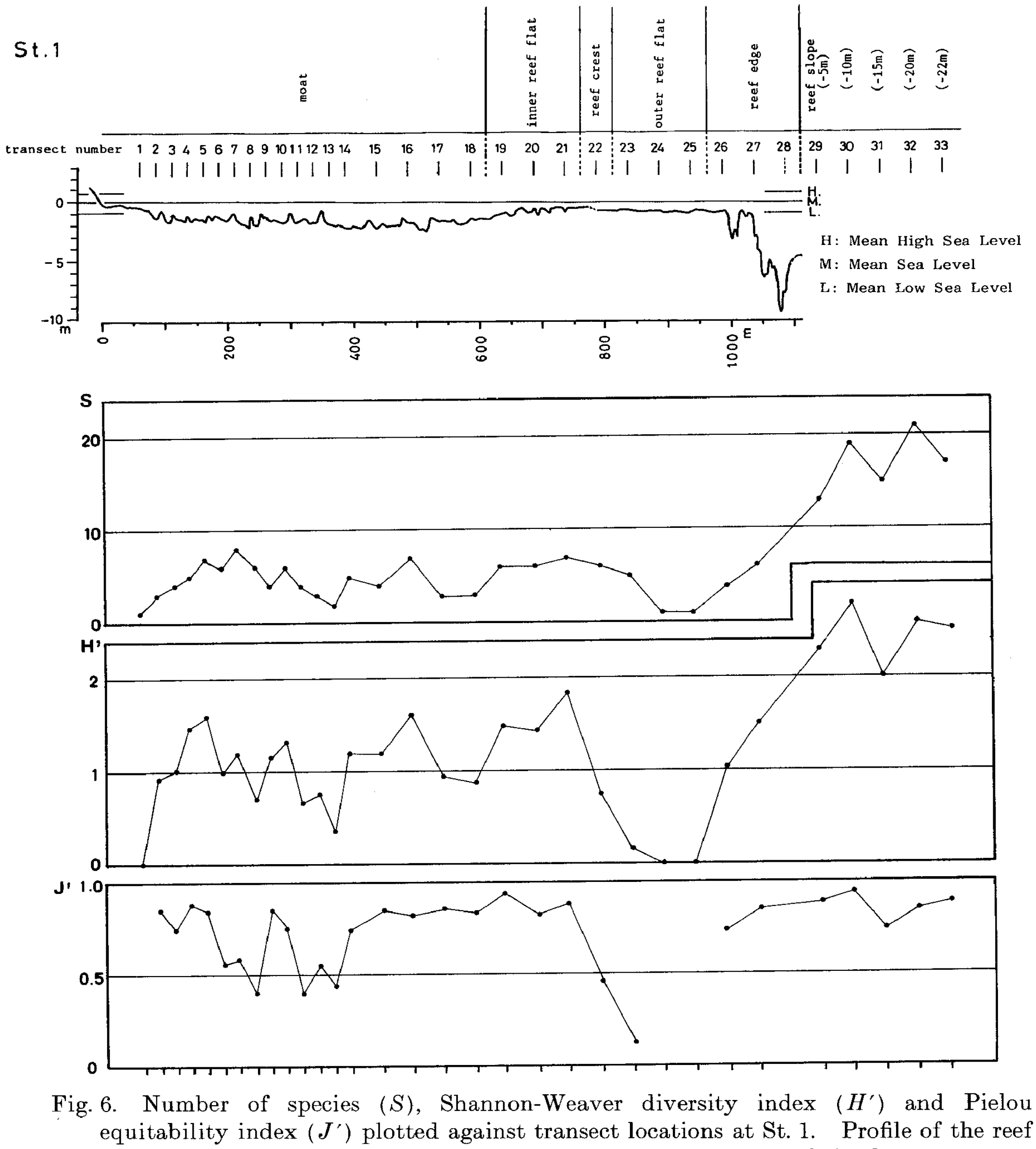


Fig. 6. Number of species (S), Shannon-Weaver diversity index (H') and Pielou equitability index (J') plotted against transect locations at St. 1. Profile of the reef at St. 1 and topographic areas are indicated in the upper part of the figure.

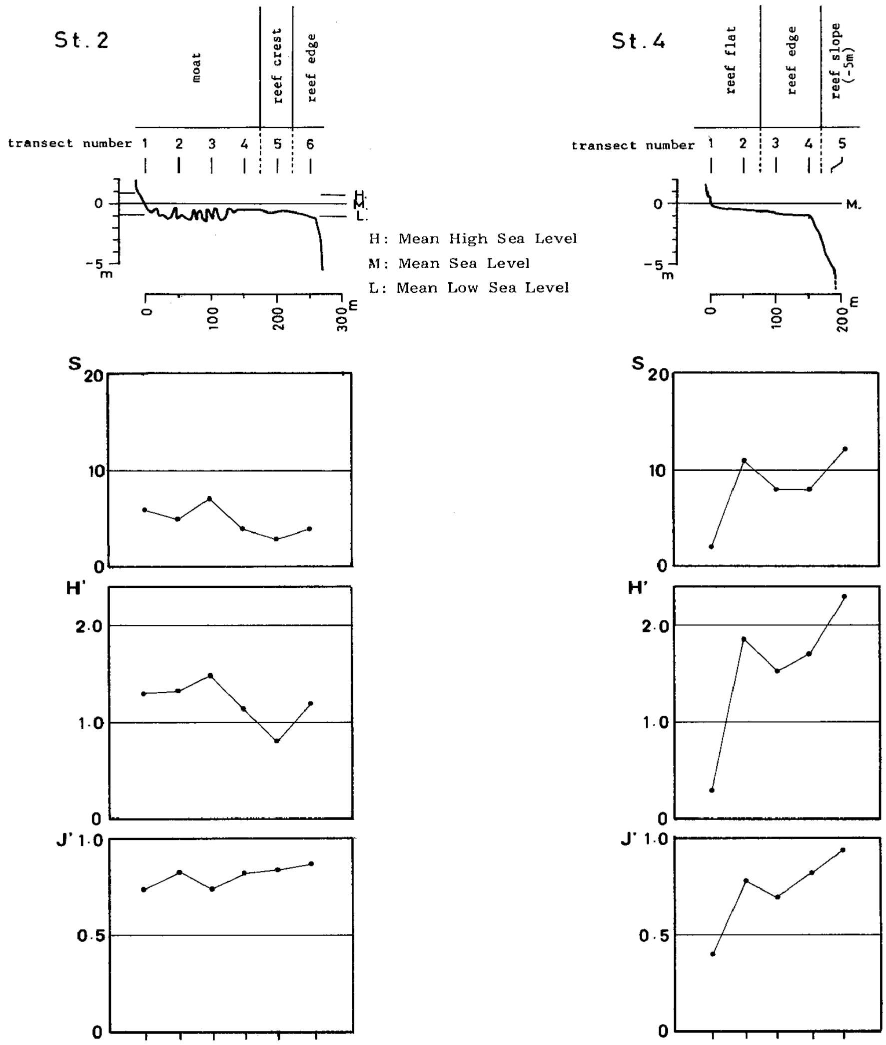


Fig. 7. Distributions of indices S, H' and J' at St. 2 and St. 4.

nation intensities to those in the surface water plotted against the water depth on the reef slopes at St. 1 and St. 4. The values decrease exponentially with the increase of depth at both stations. The absolute intensities at St. 1 are less than those at St. 4, owing to the difference of cloud density at the time of the measurements.

(2) Topography of Coral Reefs

The profiles of the coral reefs at four stations were depicted from the depth data along the fundamental lines (Figs. 6, 7 and 8). Each profile can be divided into several topographic sections. The terminology of topography here used follows to Takahashi *et al.* (1983). The coral reefs can be topographically divided into two parts. One is nearby flat and its depth ranges from 0 to a few meters. It includes moat, inner reef flat, reef crest, outer reef flat and reef edge from coast side to offshore side. The other, called reef slope, declines toward offshore at angles of about 10 to 90 degrees.

Moat The moat is adjacent to the coast. The water never dries up even at low tide. The substratum is mainly composed of organic remains of sand and gravel sizes. Tests of foraminifers, mol-

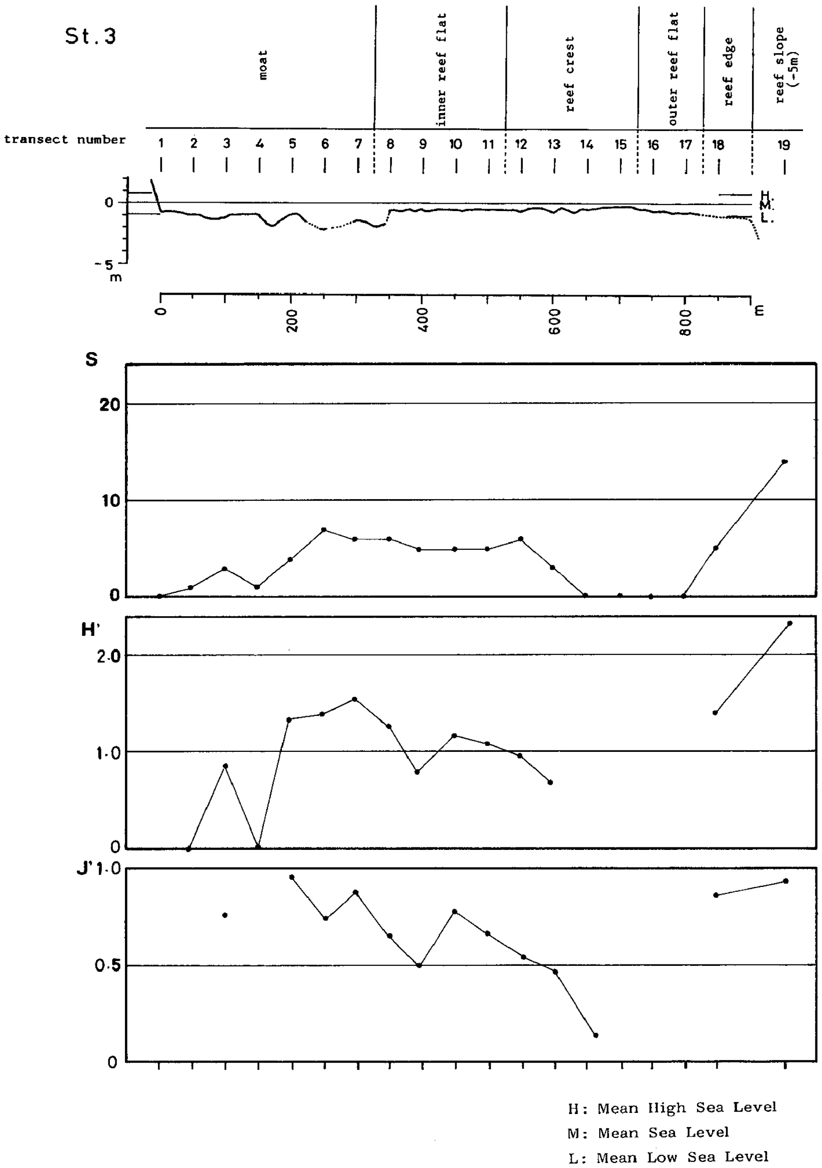


Fig. 8. Distributions of indices S, H' and J' at St. 3.

luscs, calcareous algae and corals predominate. Sea grass bushes are distributed in places. Small coral patches and microatolls can be seen in the moat.

Inner reef flat The inner reef flat is situated between the moat and reef crest. It is a low tide level plane. The substratum consists of older reef limestones. Small coral patches and microatolls are developed and often fuse together.

Reef crest The reef crest is the highest ridge which stands the outer part of the inner reef flat. In the reef crest, older limestones are exposed. In places, coral debris is abundant. A zonal distribution of supracolonies of branching or foliaceous corals is recognized.

Outer reef flat The outer reef flat is situated between the reef crest and the reef edge. It is a low tide level plane. The substratum consists of older limestones where fixed dead corals and coral debris are frequently observed. As in the reef crest, supracolonies of branching or foliaceous corals are observed.

Reef edge The reef edge is located at a boundary between the outer reef flat and reef slope. It is always situated under a low tide level and affected by waves. The substratum is composed of older reef limestones. Sands and gravels do not occur. It should be noted that no algal ridges are observed in the Ryukyu Islands.

Reef slope In the reef slope, grooves and spurs are well developed as in reefs of the other regions. Corals and encrusting calcareous algae cover the surface of spurs and walls of grooves. Sand and gravel deposits are found on the floor of grooves.

In the reefs at St. 1 and St. 3, complete sets from the moat to the reef slope mentioned above are clearly discriminated. At St. 2, inner and outer reef flats are poorly developed. At St. 4, the moat is not developed and a flat plane corresponding to the outer reef flat directly adjoins the coast.

(3) Community Structures

a. Diversity

All the hermatypic scleractinian corals recorded in this study are listed in Table 4. They comprise 47 genera and 139 species. One genus and two species belong to the hermatypic hydrozoan corals and one genus and one species to the hermatypic octocoral. Ahermatypic scleractinian corals identified consist of two genera and two species. The number of species is less than that reported by Eguchi (1975) and Yaeyama Branch of Okinawa Pref. Fisheries Exp. St. (1983), because the stations here studied are limited.

Three species diversity indices are used to express the richness and the equitability of species. They are the number of species (S), Shannon and Weaver's diversity index (H') (Shannon and Weaver, 1948) and Pielou's evenness index (J') (Pielou, 1966).

The Shannon and Weaver's formula is :

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where P_i $(=N_i/N)$ is the proportion of the total area of colonies belonging to the ith species (N_i) to the total area of all colonies (N).

The evenness index (J') is :

$$J' = H'(\text{computed in each transect})/H'_{\max}$$

$$H'_{\max} = -S\left(\frac{1}{S}\ln\frac{1}{S}\right) = \ln S$$

If the number of species in a transect is larger and every species in a transect occupies the area equally, H' will be higher values. J' takes high values if the area occupied by each species in a transect is evenly distributed.

The distributions of index S at the four stations (stations 1, 2, 3 and 4) are summarized as follows (Figs. 6, 7 and 8). In the area from the moat to the inner reef flat, five species are observed on average. The index S decreases toward the reef crest until the value becomes zero to three. It increases again in the reef edge and reaches twenty in the reef slope. The index S seems to be maximum at about 20 m in depth, although the observation of the areas deeper than 22 m was not carried out by the transect method but only by naked eyes.

The diversity index H' is related to the number of species (Figs. 6, 7 and 8). The value of H' in the moat of the four stations is approximately 1.0 and increases slightly towards the reef crest. It becomes zero suddenly in the outer reef flat and increases again in the reef edge and shows more than 2.5 in the reef slope. At St. 3, the value could not be calculated in the reef crest and the outer reef flat, where no corals are found.

The value of evenness index J' in the reef crest and the outer reef flat indicates almost zero or indeterminable, whereas that of the other areas ranges from 0.4 to 0.9 (Figs. 6, 7 and 8). The index values

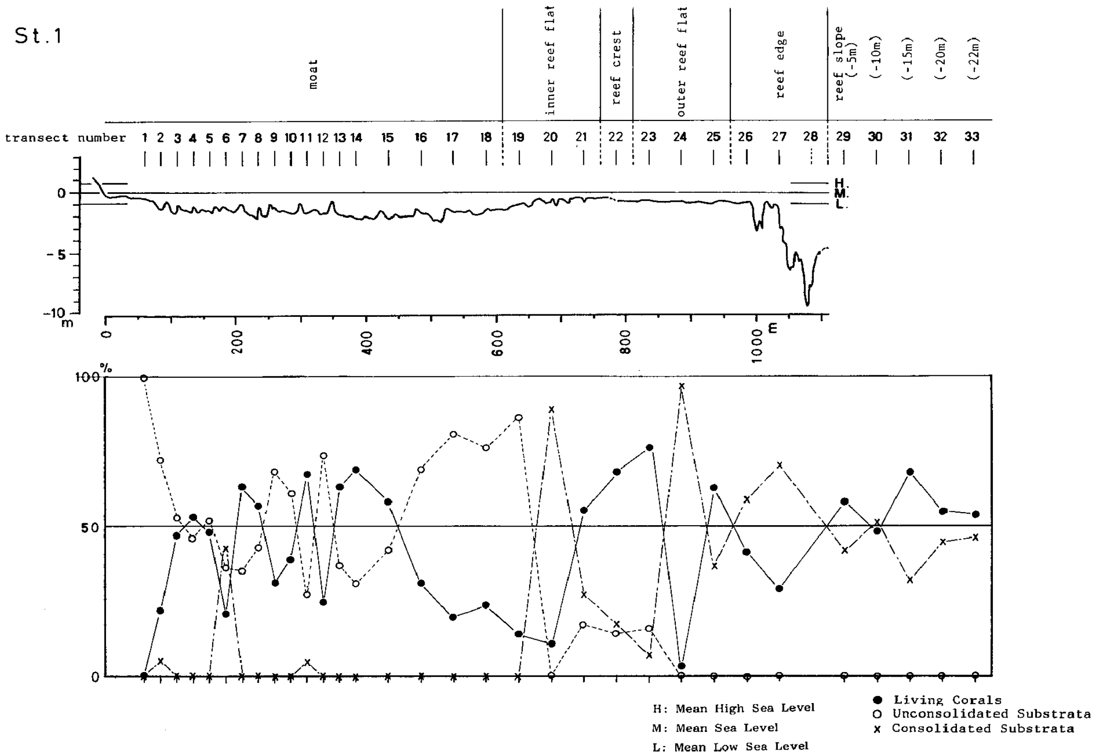


Fig. 9. Coverage rate of corals (●), unconsolidated substrata (○) and consolidated substrata (×) plotted against transect locations at St. 1.

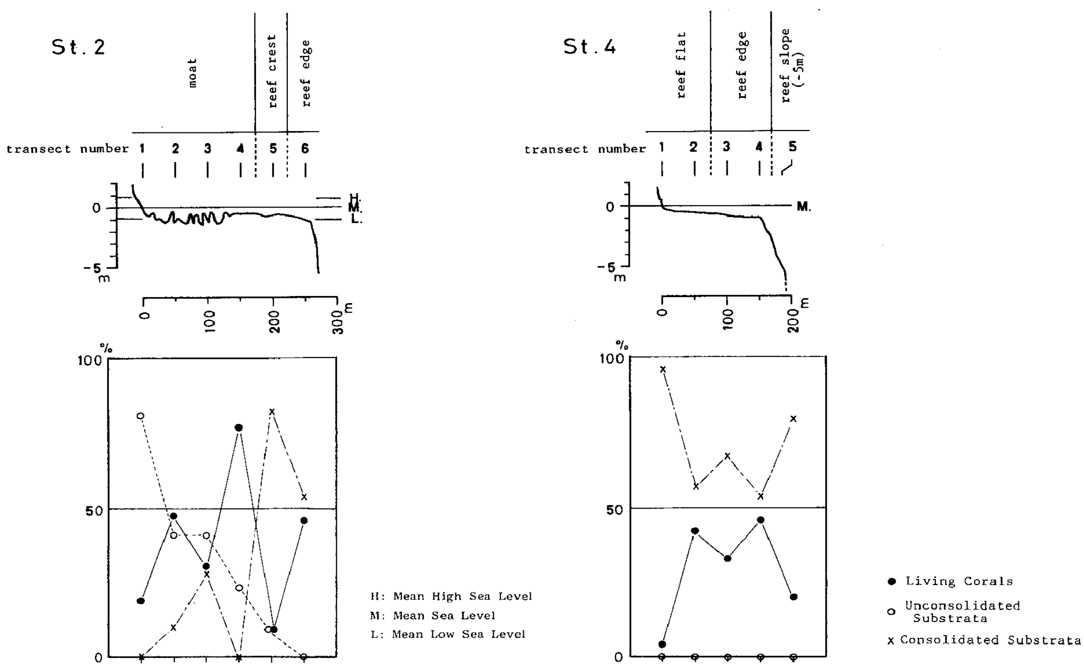


Fig. 10. Coverage rate of corals, unconsolidated substrata and consolidated substrata plotted against transect locations at St. 2 and St. 4.

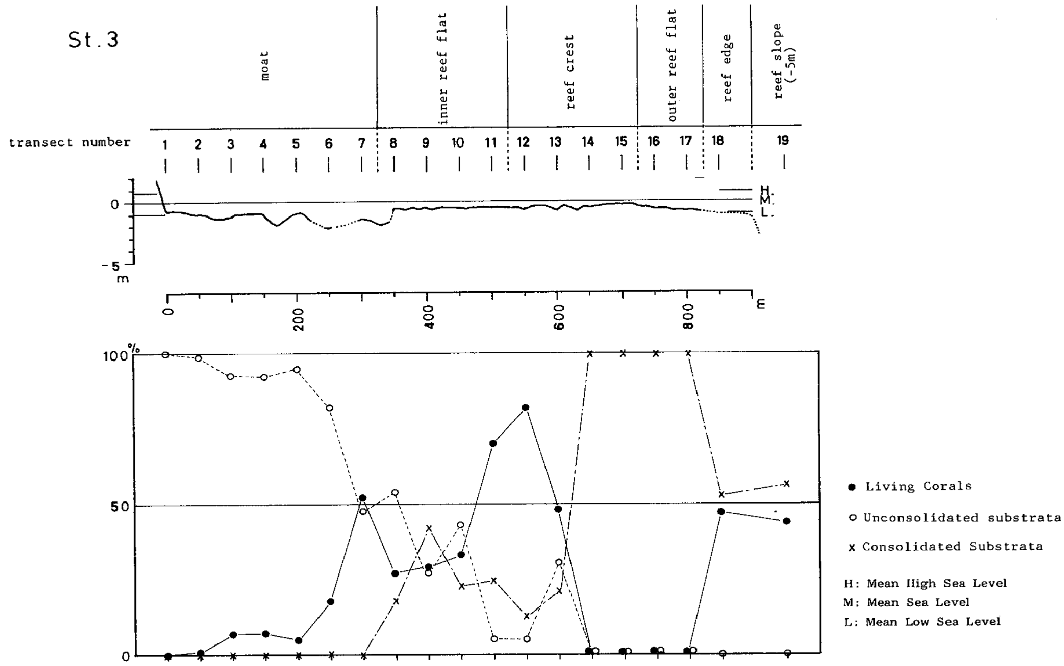


Fig. 11. Coverage rate of corals, unconsolidated substrata and consolidated substrata plotted against transect locations at St. 3.

in the inner part of the moat show large fluctuations, but the area from the outer part of the moat to the inner reef flat and reef slope has constant values.

b. Coverage

The coverage rate of the living corals, unconsolidated substrata and consolidated substrata of each transect were computed at the four stations (Figs. 9, 10 and 11). The "living corals" mean all living hermatypic corals with skeletons excluding the soft corals. Unconsolidated substrata consist of carbonate sands and gravels. Consolidated substrata are composed of old reef limestones. Fixed dead corals and encrusting calcareous algae were included in the consolidated substrata in the measurements.

The coverage rate of the living corals varies from 10 to 70% on the moat and the inner reef flat. It begins to increase in the outer part of the inner reef flat and reaches 60 to 80% on the reef crest. On the zone from the reef crest to the outer reef flat, it decreases suddenly and takes value 0. The coverage rate begins to increase again in the reef edge. It ranges from 30 to 70% in the reef slope. The range of variation is the widest in the moat (Figs. 9, 10 and 11).

Unconsolidated substrata occupy wide areas in the moat. Their coverage rate decreases gradually towards the reef crest. The unconsolidated substrata cannot be observed in the outer part of the reef crest. In the area from the moat to the inner reef flat, the unconsolidated substrata are scarcely observed. The zone from the reef crest to the reef slope consists mostly of consolidated substrata, and unconsolidated ones are found in small amounts in the zone (Figs. 9, 10 and 11).

The fixed dead corals mainly occur on the consolidated substrata in the outer reef flat and the reef edge, while the living encrusting calcareous algae are often observed on the consolidated substrata in the reef slope.

c. Community

R-mode cluster analysis was adopted in order to determine the species which accompany together quantitatively. The coverage data of each coral species

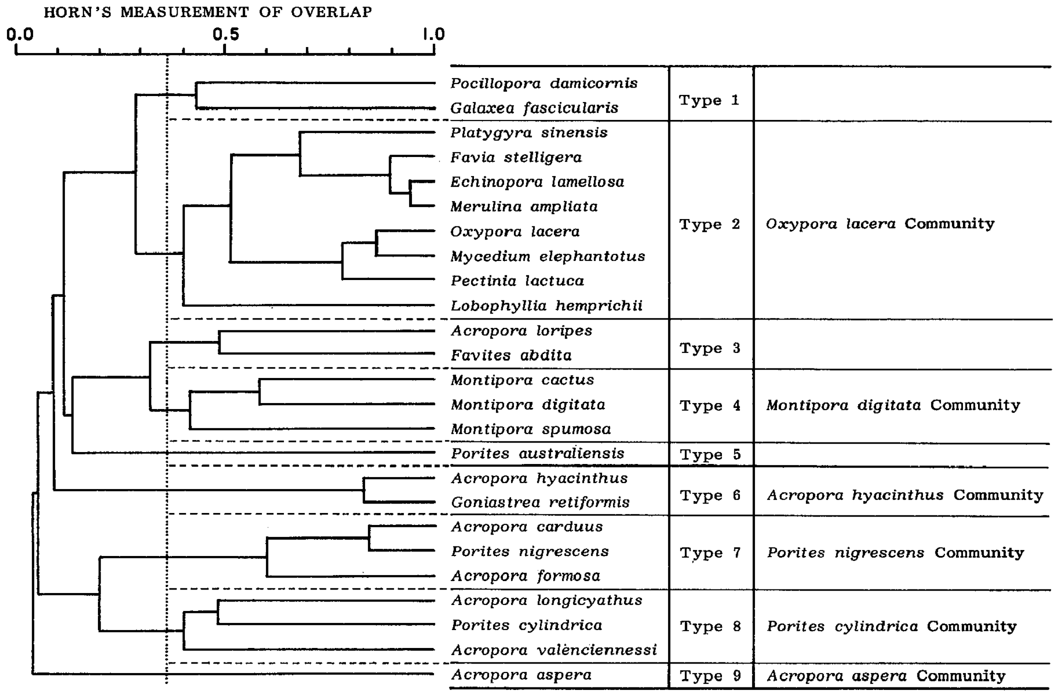


Fig. 12. Dendrogram for *R*-mode cluster analysis of corals and communities at St. 1.

at St. 1 were used for the analysis, because St. 1 provided a sufficient number of species and transects. Twenty-five species which appeared in more than three transects at St. 1 were analyzed. The distances among species were represented by Horn's measurement (Horn, 1966) of overlap (*Ro*).

The formula of *Ro* is shown bellow.

X and Y are the total length of transects X and Y. The total length of ith species in the transects X and Y are indicated as x_i and y_i. Computation was carried out with a NEAC ACOS System 1000 computer at the Tohoku University Computer Center.

Twenty-five species were clustered into nine types (Fig. 12). Of these types, Types 1, 3 and 5 were excluded from the analysis of community, because they consist of the species which show wide ranges in a reef. The other types were composed of the species which occur in a specified ecological and topological area. They were recognized as communities. Each community here is called by the name of characteristic species. They are *Montipora digitata*, *Porites cylindrica*, *Porites nigrescens*, *Acropora aspera*, *Acropora hyacinthus* and *Oxypora lacera* Communities. Their names, associated species and distributions are shown in Table 5.

Besides these communities, four communities which could not be discriminated from the cluster analysis were additionally recognized (Table 5). *Favia stelligera* Community distributes from 0 to 10 m in depth on the reef slope. This community is similar to *Oxypora lacera* Community in species composition, but lacks species of the Pectiniidae such as *Oxypora lacera* and *Mycedium elephantotus*. On the reef slope whose depth is about 30 meters, there exists a community composed of *Leptoseris* spp., *Pachy-*

$$Ro = \frac{\sum (x_i + y_i) \log (x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X+Y) \log (X+Y) - X \log X - Y \log Y}$$

Table 5. List of Recent coral communities, associated species and their distributions in the Ryukyu Islands.

Communities	Associated Species	Distributions
Montipora digitata Community	*Montipora cactus* *M. spumosa* *Porites lutea* *Goniastrea aspera*	St. 1 Inner-Middle Part of Moat St. 2 Moat
Porites cylindrica Community	*Acropora longicyathus* *A. valenciennessi* *Porites lobata*	St.1 Middle-Outer Part of Moat
Porites nigrescens Community	*Acropora carduus* *A. formosa* *Montipora foliosa* *Pavona decussata* *Euphyllia glabrescens*	St.1 Outer Part of Moat- Inner Reef Flat
Acropora aspera Community		St.1 Reef Crest-Outer Reef Flat St.2, St.3 Reef Crest St.4 Inner Part of Outer Reef Flat
Acropora hyacinthus Community	*Stylocoeniella armata* *Pocillopora verrucosa* *Acropora digitifera* *A. humilis* *A. monticulosa* *A. palmerae* *Goniastrea retiformis*	St.1 Reef Edge-Reef Slope (-3m) St.2 Reef Edge St.3 Outer Reef Flat-Reef Edge St.4 Outer Part of Outer Reef Flat- Reef Slope (-5m)
Oxypora lacera Community	*Seriatopora* sp.A *S.* sp.B *Montipora danae* *Sandalolitha robusta* *Porites lichen* *Favia stelligera* *Platygyra sinensis* *Diploastrea heliopora* *Echinopora lamellosa* *Merulina ampliata* *Lobophyllia hemprichii* *Mycedium elephantotus* *Pectinia lactuca* *Euphyllia fimbriata* *Plerogyra sinuosa*	St.1 Reef Slope (-5~-22m)
Favia stelligera Community	*Seriatopora* sp.A *S.* sp.B *Acropora divaricata* *A. microcladose* *A. palifera* (Encrusting Form) *Montipora danae* *Porites lichen* *Platygyra sinensis* *Montastrea curta* *Diploastrea heliopora* *Echinopora lamellosa* *Merulina ampliata* *Euphyllia fimbriata*	St.1 Reef Slope (0~-10m) St.3 Reef Slope (0~-5m)
Leptoseris scabra Community	*Leptoseris hawaiiensis* *L. mycetoseroides* *Pachyseris speciosa*	St.1 Reef Slope (-30m~)
Heliopora coerulea Community	*Montipora digitata* *M.* sp.A	St.3 Moat-Crest
Anacropora spinosa Community	*Acropora echinata* *Leptoseris scabra* *Porites cylindrica*	Kabira Cove

seris speciosa and other foliaceous or laminar corals. It is named *Leptoseris scabra* Community in this paper. At St. 3, *Heliopora coerulea* Community containing *H. coerulea*, *Montipora digitata* and *M.* sp. A is observed on the area from the moat to the reef crest. A peculiar community which is usually seen in the dark and quiet places is distributed in the Kabira Cove. It is here called *Anacropora spinosa* Community.

The distributions of the communities are generally limited in specific ecological and topographical areas, although some communities coexist in places ; for example, the *Porites cylindrica* Community and the *Porites nigrescens* Community are found together on some places of the moat.

In contrast, different communities were found in the same topographic parts of two different areas. For example, physical features such as water temperature, wave energy and light intensity in the moat of St. 3 are equivalent to those of St. 1. But the *H. coerulea* Community occurs in the moat of St. 3, while the *P. cylindrica* and the *P. nigrescens* Communities are found in that of St. 1.

(4) Growth Form

Various growth forms are discriminated among the living hermatypic corals. Eleven types of the outer shapes were recognized in this study. Subdivisions and terminology of the shapes are shown

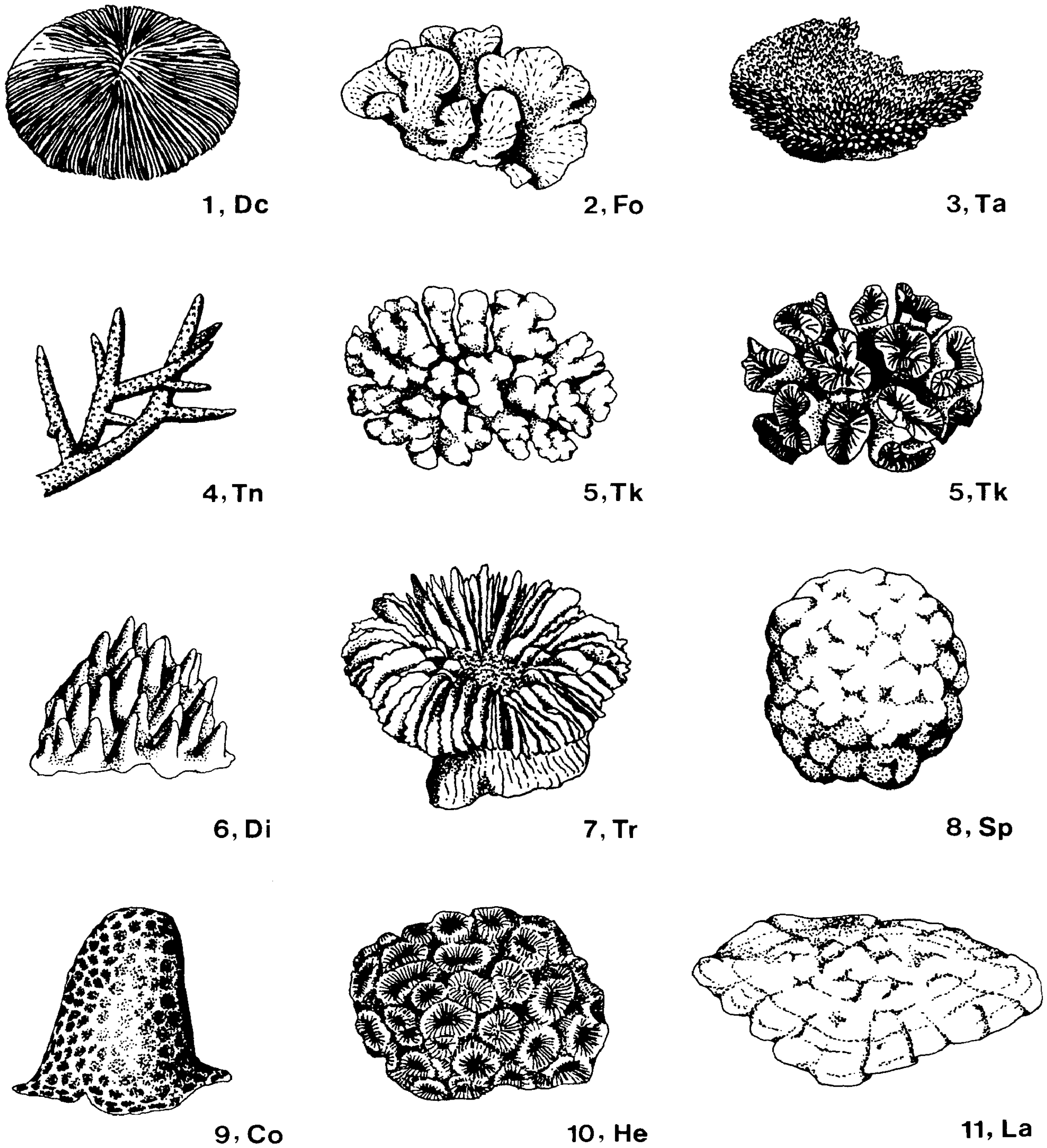


Fig. 13. Growth forms of hermatypic corals. Abbreviations are explained in Table 6.

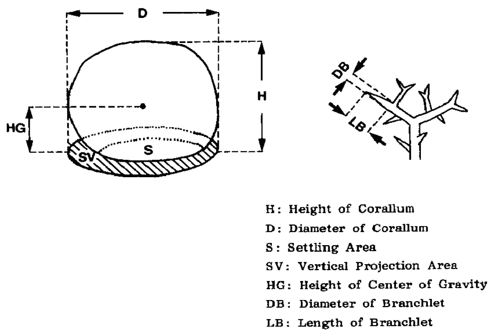


Fig. 14. Explanation of terms used in Table 6.

in Table 6, Figs. 13 and 14 and as follows.

I. Unattached .... *discoidal*
II. Attached
  A. Growth centers numerous
    1. Vertical projection area exceeds settling area
      a. Unbranched ...... *foliaceous*
      b. Branched
        b-1. Branches on plate .... *tabular*

Table 6. Classification and terminology of growth form of hermatypic corals. Terms are explained in Fig. 14.

<table>
<tr><td>Unattached</td><td colspan="5"></td><td>Discoidal (Dc)</td></tr>
<tr><td rowspan="10">Attached</td><td rowspan="5">Growth Centers Numerous</td><td rowspan="4">SV>S</td><td>Unbranched</td><td colspan="2"></td><td>Foliaceous (Fo)</td></tr>
<tr><td rowspan="3">Branched</td><td>Branches on Plate</td><td></td><td>Tabular (Ta)</td></tr>
<tr><td rowspan="2">Dendritic Branches</td><td>LB/DB>3</td><td>Thin (Tn)</td></tr>
<tr><td>LB/DB≦3</td><td>Thick (Tk)</td></tr>
<tr><td>SV=S</td><td colspan="3"></td><td>Digitate (Di)</td></tr>
<tr><td rowspan="5">Growth Center single or indistinguishable</td><td rowspan="2">SV>S</td><td>HG>H/2</td><td colspan="2"></td><td>Trocoid (Tr)</td></tr>
<tr><td>HG≦H/2</td><td colspan="2"></td><td>Spherical (Sp)</td></tr>
<tr><td rowspan="3">SV=S</td><td>H/D≧1</td><td colspan="2"></td><td>Columnar (Co)</td></tr>
<tr><td>1/10≦H/D<1</td><td colspan="2"></td><td>Hemispherical (He)</td></tr>
<tr><td>H/D<1/10</td><td colspan="2"></td><td>Laminar (La)</td></tr>
</table>

b-2. Branches dendritic

b-2-1. LB/DB exceeds 3 .... *branches thin*

b-2-2. LB/DB less than 3 .. *branches thick*

2. Vertical projection area equal to settling area........ *digitate*

B. Growth center single or indistinguishable

1. Vertical projection area exceeds settling area

a. HG exceeds $H/2$ .. *trochoid*

b. HG less than $H/2$ *spherical*

2. Vertical projection area equal to settling area

a. H/D ratio exceeds 1 .... *columnar*

b. H/D ratio between 1 and 1/10.......... *hemispherical*

c. H/D ratio less than 1/10 .... *laminar*

Figures 15, 16 and 17 indicate the

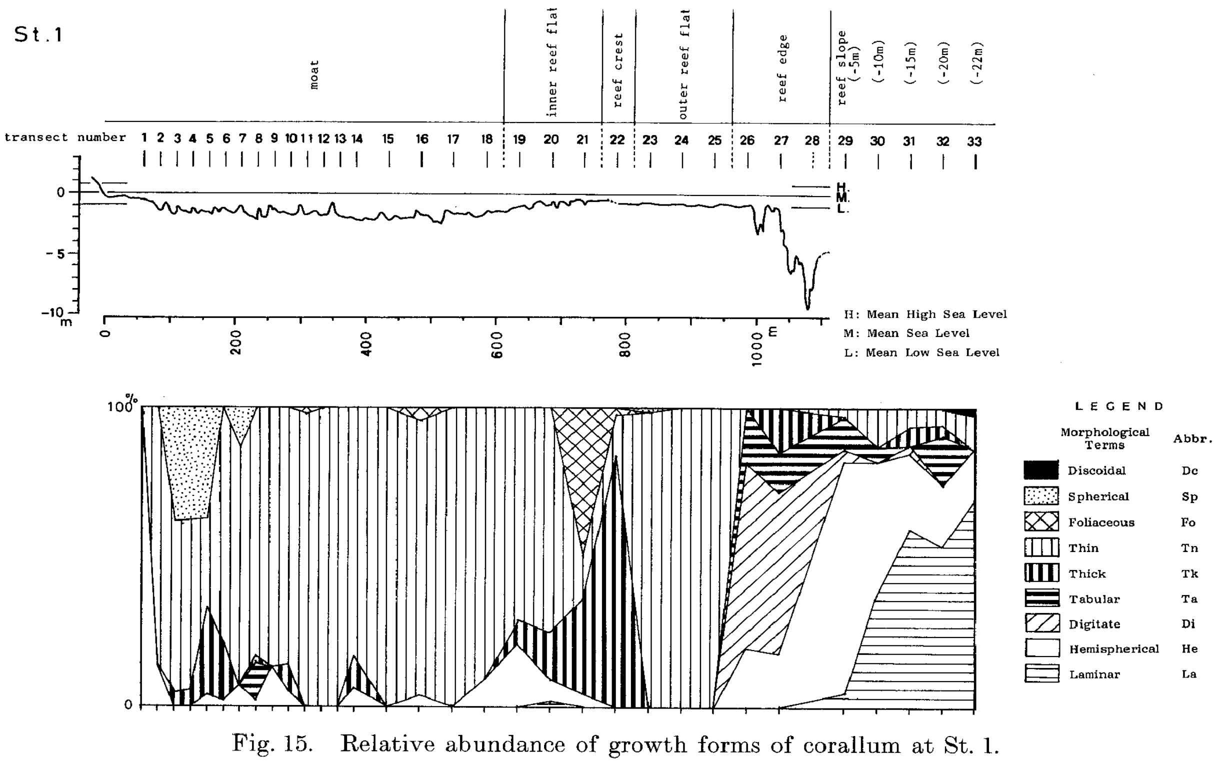


Fig. 15. Relative abundance of growth forms of corallum at St. 1.

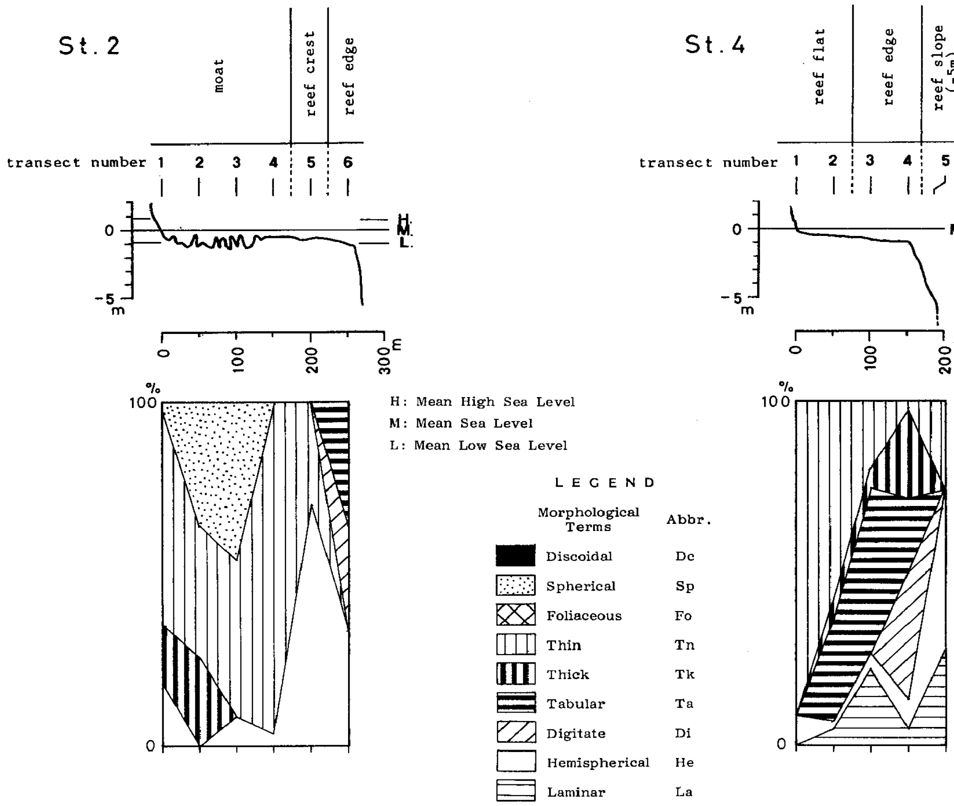


Fig. 16. Relative abundance of growth forms of corallum at St. 2 and St. 4.

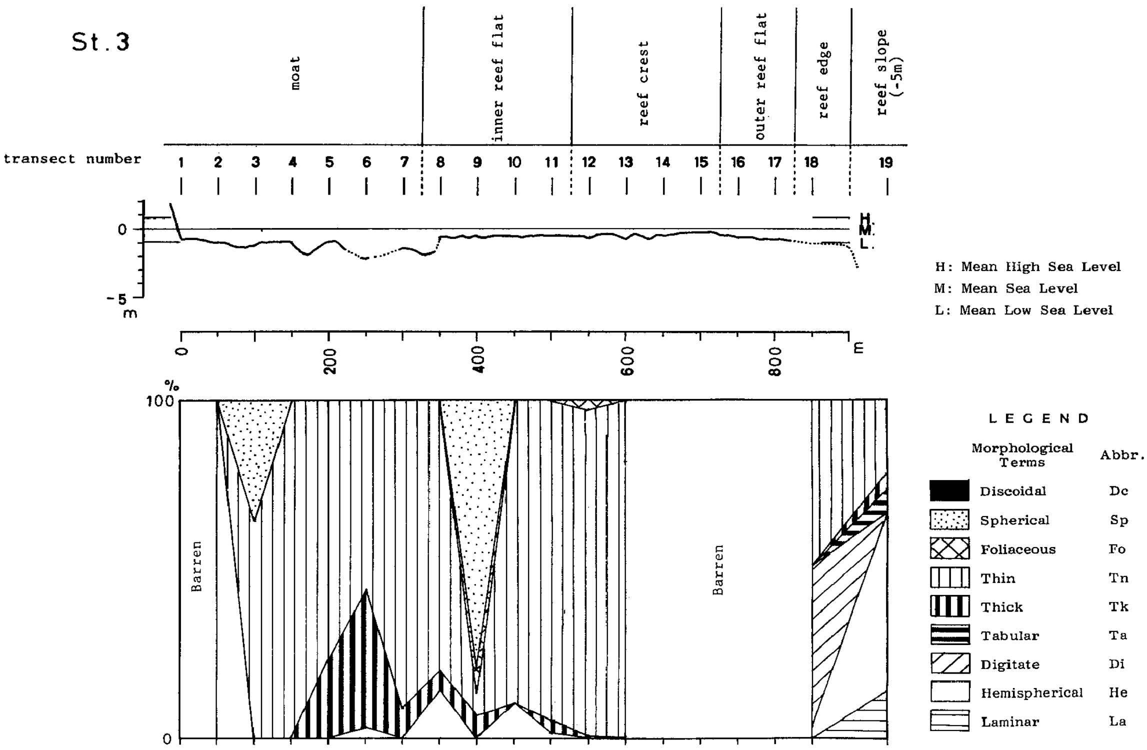


Fig. 17. Relative abundance of growth forms of corallum at St. 3.

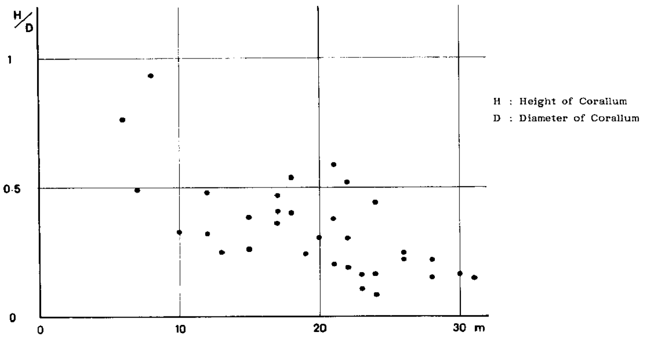


Fig. 18. Height/diameter ratio of coralla of *Porites australiensis* (H/D) plotted as a function of depth at St. 4.

frequency of each growth form at stations 1-4. The frequency is shown by the percentage coverage of the colonies belonging to each type in the transects. It is clear that the morphologies of the coralla are intimately related to the topographic areas where they are found. Thin branching colonies associated with colonies having thick branching, foliaceous, spherical and hemispherical shapes predominate from the moat to the outer reef flat. They often construct microatolls. Most colonies in the reef crest and the outer reef flat are often of branching and foliaceous types. They frequently make supracolonies. The colonies whose shapes are tabular and digitate excel in the outer reef flat and the reef edge. Thick branching and hemispherical colonies occupy most areas ranging from 0 to 10 m in depth, while laminar colonies are more dominant than hemispherical ones in the area deeper than 10 m. Judging from the observation by naked eye, most colonies at a depth of 30 m are of laminar and foliaceous types.

Variations of growth form within a species are observed in *Porites australiensis*, *P. lutea*, *P. lobata*, *Favia stelligera*, *Favites abdita* and *Cyphastrea* spp. There is a general tendency that the colonies become spherical in the shallower water and laminar in the deeper one within a single species. Figure 18 shows the relation between the ratio of height and diameter of corallum and water depth of *P. australiensis* at St. 4. It clearly indicates that the growth form becomes flatter as the depth increases.

Two parameters were measured in order to make a model to explain the mechanism of variations of the growth forms. They are the annual growth rate of corallum and the annual increasing rate of surface area which bears living tissue.

Colonies of three species of the genus *Porites* at St. 1, St. 4 and Yoan were chosen for the measurement, because they are abundant through the wide range of water depth. They were collected from the moat to the reef slope (0

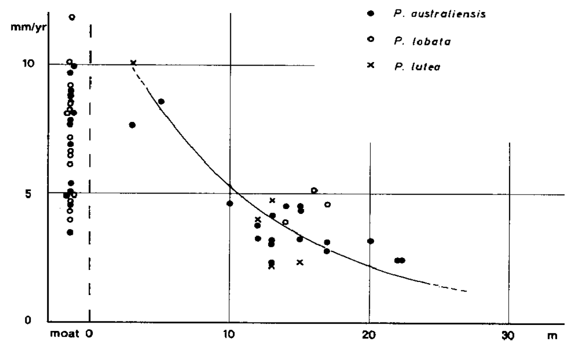


Fig. 19. Growth rate (mm/yr) of *Porites australiensis* (●), *P. lobata* (○) and *P. lutea* (×) as a function of depth at St. 1. Line drawn in the figure is an exponential regression curve of depth to growth rate exclusive of data from moat.

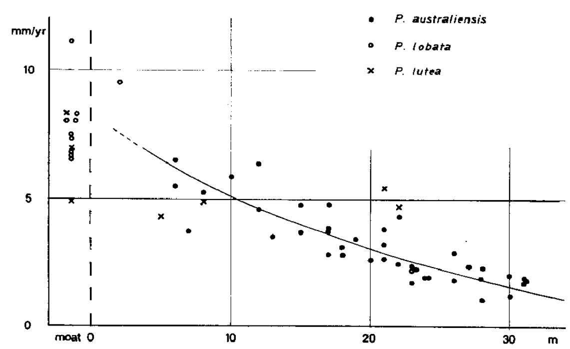


Fig. 20. Growth rate of *Porites australiensis*, *P. lobata* and *P. lutea* as a function of depth at St. 4.

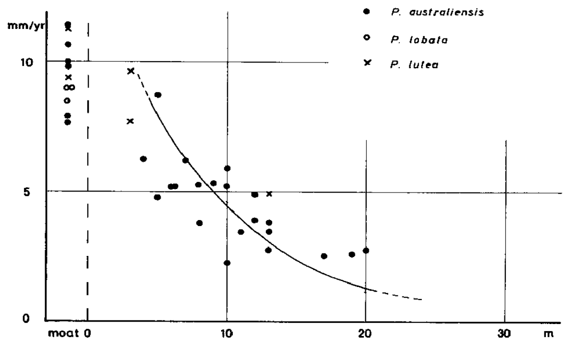


Fig. 21. Growth rate of *Porites australiensis*, *P. lobata* and *P. lutea* as a function of depth at Yoan.

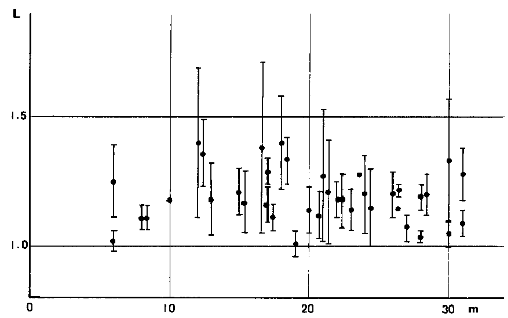


Fig. 22. Increasing rate of surface area of *Porites australiensis* as a function of depth at St. 4. Bars indicate standard error ($\pm 1\sigma$).

to 30 m in depth).

The x-radiographs of the coral specimens from the depth 0, 13, and 30 m are shown in Plate 27. A pair of dark and light concentric bands is an annual ring of a corallum. Annual growth rate is indicated by the mean width of a pair of density bands. Annual increasing rate of surface area is the mean ratio of the length of a density band in a year to that in the next year.

Relations between annual growth rate of three species and water depth are shown in Figs. 19, 20 and 21. Among the species, *Porites australiensis* is found most widely distributed from the moat to the reef slope. So, the values of the growth rate and the increase in rate of *P. australiensis* were used for the model. The annual growth rate of *P. australiensis* decreases in proportion to the depth. The growth rates of *P. lobata* and *P. lutea* do not contradict those of *P. australiensis*.

The growth rates of *P. australiensis* at each depth are similar in three regions in spite of the difference of mean annual temperature.

The annual increase in rates of surface area (Fig. 22) were measured at St. 4. It can be said that the rate is constant regardless of depth.

4. Discussion

Diversity

So far as the study on the distribution of diversity within a reef is concerned, it is difficult to compare the values of diversity indices directly between various regions, because the indices are affected by regional differences in the coral fauna and sample size. But the trend of diversities in a reef is thought to be comparable among reefs, since it is not controlled by the richness of species.

Although diversity of corals has been represented by many indices such as the number of species, Simpson's index, Shannon and Weaver's index (H') and equitability, these indices have the same trend within a reef (Loya, 1972; Porter, 1972; Figs. 6, 7 and 8 in this thesis). Therefore, those in different regions may be discussed together.

Recently, many data on the diversity have been reported from the reef slope. Sheppard (1982) divided them into two distribution patterns within a reef. The first pattern shows a general decline of diversity with depth. It was observed also in Bikini (Wells, 1954), Phoenix Islands (Dana, 1979) and Maldives (Rosen, 1975). The second pattern has a peak of diversity at depths from 20 to 30 m. It was reported also in Eilat (Loya, 1972), Chagos (Sheppard, 1980), Fanning Island (Maragos, 1974), Panama (Porter, 1972) and Discovery Bay (Goreau and Goreau, 1973). Sheppard (1982) generalized the second pattern and mentioned that there is the highest diversity point at a quarter depth of the whole depth range of hermatypic corals.

At St. 1, St. 2 and St. 3, diversity indices indicate a bimodal pattern; the lowest peak between them is located on the outer reef flat (Figs. 6, 7 and 8). One mode is found from the moat to the inner reef flat. The other mode is situated at 10 to 20 m in depth of the reef slope. The peak of the latter mode is higher than the former one. Consequently, the distribution pattern of diversity in the reef slope at St. 1 can be correlated with the pattern modified by Sheppard (1982). The low value in the outer reef flat is due to the facts that the wave agitation is very strong and the flat floor exposes frequently in low tide. A few patches in this area are almost monopolized by a single species, *Acropora aspera*, which grows fastest among the hermatypic corals. Although the coverage rates in both areas where the two modes are observed are equal as mentioned later, H' values of the outer peak are about two times those of the inner peak. Therefore, it seems that the reef slope provides the optimum condition for coral growth in the sense of niche partitioning.

Coverage

Changes of coverage rate in a reef were investigated in various regions (Barnes *et al.*, 1971; Loya and Slobodkin, 1971; Maragos, 1974; Bak, 1977; Van den Hoek *et al.*, 1978; Sheppard, 1980; Bouchon, 1981). The greater parts of them have a similar pattern and can be summarized as follows. The coverage rate increases with depth from 0 to 20 m in depth. It reaches more than 50% from 20 to 30 m. In the deeper reef slope, the rate begins to decrease. Chappell (1980) noted that the carbonate production rate is the highest in the reef slope from 20 to 30 m, affected by the amount of illumination and the restriction of hydrodynamic energy and sedimentation.

Bimodal distribution patterns of coverage rate in a reef were also recognized at St. 1, St. 2 and St. 3 (Figs. 9, 10 and 11). The lowest value of coverage was recorded in the outer reef flat as in the case of diversity. The highest peak of one mode is situated in the reef crest, just adjacent to the outer reef flat. The corals such as *Acropora aspera* and *Pavona* spp. which occupy the most part of the coverage of this area make the supracolonies. On the other hand, the coverage rate suddenly increases and attains 50% from the outer reef flat to the reef edge. It is constant from the reef edge to the reef slope (20 m in depth) and begins to decrease from 30 m at St. 1 (Fig. 9). The tendency of the coverage rate in the reef slope at St. 1 is somewhat different in having no clear peak compared with the reefs of the other regions.

It is known that the highest value of coverage often reaches 70% on the reef slope of many coral reefs (Barnes *et al.*, 1971; Loya and Slobodkin, 1971; Sheppard, 1980; Bouchon, 1981; Dollar, 1982; Grigg, 1983). However, it is less than 60% at St. 1. The low value is considered to be due to the lower water temperature in the Ryukyu Islands.

The coverage rate in the moat is equivalent to that in the reef slope. But the carbonate production rate on the moat is much higher than that in the reef slope, because the most corals in the moat, namely, *Acropora* spp., *Montipora* spp. and *Porites* spp. grow faster than the other corals.

Relationship between Diversity and Coverage

Connell (1978) discussed the models which explain the local diversities, and proposed six hypotheses standing on two points of view. One standpoint is that the communities never reach the equilibrium; in other words, a high diversity results in continuous disturbance of envi-

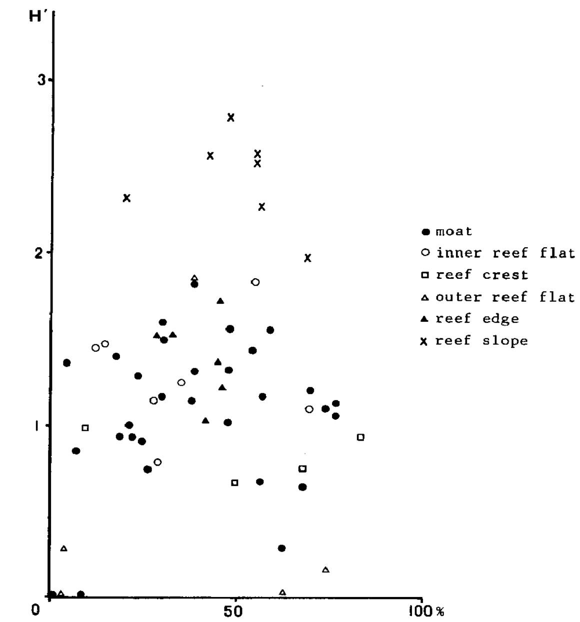


Fig. 23. Coral species diversity (H') plotted against coral coverage rate in each topographic area.

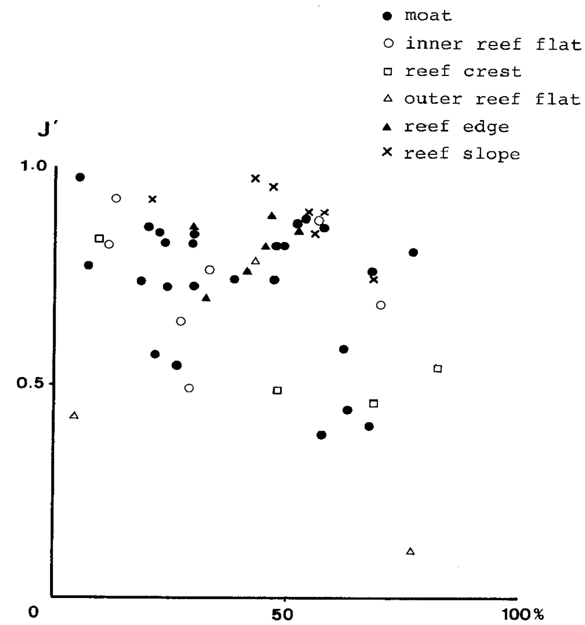


Fig. 24. Coral species equitability (J') plotted against coral coverage in each topographic area.

ronments. The other is the opposing hypothesis that a high diversity is maintained in the various equilibrium. He mentioned that the high diversity of reef corals can be elucidated by the intermediate disturbance hypothesis which assumes the nonequilibrium situation.

The intermediate disturbance hypothesis is defined as follows. The diversity increases in the first stage of ecological succession. It attains the highest before the succession reaches the climax, and at last, it decreases in the climax stage by monopolization of dominant species in competition. If the disturbances come about too frequently, the diversity must stay in the first stage of the succession. If the intervals of disturbances are too long, the succession easily reaches the climax and the diversity stays in the low level. Consequently, high diversities are obtained when the disturbances have intermediate frequency. Similarly, the high diversities are supposed to be maintained when the size of the disturbances or the areas where the disturbances influence are intermediate. According to the mechanisms mentioned above, the high diversities in the coral reefs are achieved by the intermediate disturbances in frequency, size and extent.

Connell (1972) and Grigg and Maragos (1974) reported that there is a negative correlation between the coverage rate and the diversity. If the coverage rate of a community is supposed to correlate the age of the community, the negative correlations mean that the mature communities have the low diversity. In order to prove the hypothesis, Dollar (1982) investigated the difference of coverage before and after a storm. Grigg (1983) discussed the relation between the diversity and coverage and mentioned that the disturbance is important to maintain the high diversity.

Figures 23 and 24 indicate the species diversity indices H' and J' plotted against the coverage at St. 1, St. 2, St. 3 and St. 4. The plots are expressed by the symbols in every topographical area.

In Figure 23, plots of the values in the inner reef flat, the reef crest, the outer reef flat and the reef edge do not indicate a clear tendency, because the measurements of these values are not enough. But, in the moat and the reef slope, H' is low when the coverage is low. It attains the highest when the coverage is about 50%, and it decreases as the coverage exceeds 50%.

Pielou's Equitability Index J' and the coverage indicate weak negative correlations in most topographical areas (Fig. 24). It means that J' may decrease as the coverage increases.

In the ecological succession, an older community is supposed to have a larger coverage rate than does a younger one, if they inhabit similar environments. Therefore, the coral communities at Stations 1-4 are thought to have low diversity in early stage of the succession, the highest in middle, and low in late. Besides, they are monopolized by dominant species as they become older. These results support the intermediate disturbance hypothesis.

Community

Zonations of corals related to the reef topography have been made in a lot of reefs using dominant species (Wells, 1954 ; Goreau, 1959 ; Goreau and Goreau, 1973 ; Sheppard, 1981 ; Dollar, 1982), cluster analysis (Loya, 1972 ; Maragos, 1974 ; Done, 1977), the colony morphology (Barnes *et al*., 1971) and *Acropora* species (Wallace and Dale, 1977). As mentioned in the foregoing sections, 11 communities were discriminated in this study. The communities ties are generally correlated to the zones previously proposed in the Ryukyu Islands and other regions of the Pacific.

In the Ryukyu Islands, Yamazato (1969, 1971) divided the reef slope into three zones based on the distribution range of the hermatypic corals. He proposed the surface layer zone, the middle layer zone and the deep layer zone, and stated that they range from 0 to 15 m, from 15 to 50 m and from 50 to 100 m in depth, respectively.

The reef edge and upper part of the reef slope where the *Acropora hyacinthus* Community and the *Favia stelligera* Community develop are correlated to the surface layer zone. The middle layer zone corresponds to the range of the *Oxypora lacera* Community. The species in the deep layer zone are identical with those of the *Leptoseris scabra* Community.

In Kerama Islands, Eguchi (1974) recorded the coral species which can be correlated to the *Porites cylindrica* Community and the *P. nigrescens* Community. A community which contains the species of branching *Acropora* and *Porites* was observed in the moat of Yoron-to (Hirata, 1975). It can be correlated to the *P. cylindrica* and *P. nigrescens* communities. Hirata (*op. cit.*) also recognized a community equivalent to the *Acropora hyacinthus* Community in the reef slope.

Thus, most communities previously reported in the Ryukyu Islands are comparable to those in this study.

Wells (1954) reported eight zones in the outer reef of Bikini Atoll. In the moat, he recognized the *Porites lutea* zone, the *Heliopora coerulea* zone and the *Acropora palifera* zone. Their species composition correspond to that of the *Heliopora coerulea* Community which was found in the moat at St. 3. The *Acropora digitifera* and *A. cuneata* zones are distributed in the area from the inner reef flat to the reef edge of Bikini Atoll. They consist partly of the same species of the *Acropora hyacinthus* Community. In the reef slope of Bikini, Wells (*op. cit.*) proposed the *Echinophyllia*, *Leptoseris* and *Sclerhelia-Dendrophyllia* zones. The *Echinophyllia* and *Leptoseris* zones contain common species found in the *Oxypora lacera* and *Leptoseris scabra* communities, respectively. The facts indicate that the distribution and the composition of the species in the communities of the Ryukyu Islands resemble those of Bikini Atoll. But the boundary between the *Echinophyllia* zone and the *Leptoseris* zone is about 50 m in depth and is much deeper than the equivalent boundary in the Ryukyu Islands.

Besides Bikini, the communities which have similar distributions and compositions of species are known in the Samoa Islands (Mayor, 1924), Great Barrier Reef (Manton, 1935; Done, 1982), Nicobar Islands (Scheer and Pillai, 1974) and Maldive Archipelago (Pillai and Scheer, 1976). The communities in Madagascar (Pichon, 1978) and Réunion Island (Bouchon, 1981), Indian Ocean are different from those in the Ryukyu Islands. However, so far as the genera of the communities are concerned, they greatly resemble those in the Ryukyu Islands.

On the other hand, the greater part of species in Eilat (Loya and Slobodkin, 1971) and Fanning Atoll (Maragos, 1974) are the same as those of the Ryukyu Islands, but the prevailing species of the communities are different from those in this study. Communities in Hawaii Islands and Galapagos Islands are mainly composed of species which are not seen in the Ryukyu Islands (Vaughan, 1918; Dollar, 1982; Glynn and Wellington, 1983).

Generally speaking, the communities in the Ryukyu Islands are correlated to those in the centers of diversity such as Micronesia, Great Barrier Reef and Maldive Archiperago, and differ from those in the peripheral regions of coral distributions in the Indo-Pacific districts (Wells, 1954; Rosen, 1971).

Growth Form

As mentioned in the previous chapter, morphological groups of the growth forms in St. 1, St. 2, St. 3 and St. 4 are much related to the topography (Figs. 15, 16 and 17). The results of the present investigation are identical with those of the previous studies (Hirata *et al.*, 1971; Yamazato, 1971; Suzuki, 1972; Eguchi, 1974; Hirata, 1975, 1980; Horikoshi, 1979; Yamazato *et al.*, 1980). Although some communities in the moat of Ohama, Ishigaki-jima consist of different species belonging to the genus *Pavona* from those of St. 1, St. 2 and St. 3, they are composed of branching, foliaceous and spherical colonies (Takahashi and Koba, 1978). Yamazato *et al.* (1982) reported the coral communities in the upper part of the reef slopes in Uotsuri-jima. The species compositions differ from those in this study, but they have hemispherical, laminar and thick branching forms, which are similar to the forms of the corals in the reef slope at St. 1, St. 3 and St. 4 (Figs. 15, 16 and 17). Therefore, it is concluded that the distribution pattern of the morphologies of corals are nearly the same throughout the coral reefs in the Ryukyu Islands, nevertheless species compositions are different in places.

Similar patterns are recognized also in many reefs of the Pacific. For example, in the moat of Bikini Atoll, thin branching, foliaceous and spherical colonies of the genera *Acropora*, *Montipora* and *Porites* occur (Wells, 1954). The tabular and digitate forms predominate the reef edge, and the laminar form the deeper part of the reef slope (Wells, *op. cit.*). Moreover, these patterns are discerned not only in reefs which have similar communities but also in reefs containing different communities such as in Aldabra, Madagascar and Réunion (Mayor, 1924; Manton, 1935; Done, 1982; Scheer and Pillai, 1974; Pillai and Scheer, 1976; Barnes *et al.*, 1971; Bouchon, 1981; Pichon, 1978). Even in the reefs in the Atlantic Ocean, the equivalent distributions of outer shapes are reported in Jamaica (Goreau, 1959) and Curaçao (Bak, 1977). But, the reefs of the Atlantic differ from those of the Ryukyu

Islands in that a thick branching coral, *Acropora palmata*, predominates the upper part of the reef slope.

Ecomorphology of Growth Form within a Species

It is well known that some hermatypic coral species have an ecomorphology of growth shape. Goreau (1959, 1963) reported that the growth form of *Montastrea annularis* is spherical in several meters, columnar in 20 m and laminar deeper than 30 m in depth in Jamaica and thought that the change of the growth forms is due to the decrease of illumination intensity. Similar observations were made on the species not only in the Atlantic Ocean (Goreau, 1959) but in the Pacific Ocean (Yonge, 1931; Kawaguchi and Sakamoto, 1948) as well.

Recently, the ecomorphology was explained by the relationship between the illumination intensity and the growth rate of corallum (Barnes and Taylor, 1973; Chalker and Taylor, 1975; Dustan, 1975, 1979; Jaubert, 1977, 1981; Highsmith, 1979). Graus (1977) and Graus and MacIntyre (1976, 1982) simulated the growth form of *Montastrea annularis* with the computer on the basis of the alteration of illumination intensity related to depth and angles of the surface of corallum. Graus and MacIntyre (1982) mentioned that there was no genetic difference among the colonies which have different outer shapes in *M. annularis* by the transplantation of colonies.

The variation of growth form of *Porites australiensis* differs from that of *Montastrea annularis* as follows. The growth forms of *P. australiensis* are spherical in shallow places, hemispherical in intermediate depths and laminar in deeper places in a reef (Fig. 18), while the growth forms of *M. annularis* are spherical in shallower places, columnar in intermediate depths and laminar or foliaceous in deeper places (Graus and MacIntyre, 1976).

The mechanism which makes the variation of growth forms of *Porites australiensis* is thought to be different from that of *Montastrea annularis*. Graus and MacIntyre (1976) mentioned that the variation of the growth form of *M. annularis* is due to the difference of light intensity which a coral receives within a corallum. The growth rate of a corallum of *M. annularis* is highest on the top of the corallum where the strongest light intensity is obtained within a corallum (Graus and MacIntyre, 1976), while the growth rate of a corallum of *P. australiensis* is highest on the flank in some cases.

In order to interpret the mechanism of the change of the growth form of *P. australiensis*, I introduced a model using two parameters, namely, the growth rate on the top of the corallum and the increasing rate of the surface area of corallum. The model was made based on the following conception.

The carbonate production rate of the hermatypic corals seems to be proportional to the amount of the products of photosynthesis (Goreau, 1963). The photosynthesis rate is generally proportional to illumination intensity except in conditions of very high and very low intensity. The distribution of the radiance in water is expressed by an exponential equation of the depth (Jerlov, 1976). The illumination intensity is considered to be proportional to that of radiance. Hence, the annual carbonate production rate is formulated by an exponential function of the depth. Since the annual production rate can be regarded proportional to the growth rate of corallum, the value of the growth rate on the top of corallum instead of the production rate was used in the simulation. The equation of the growth rate on the top of corallum (r) is:

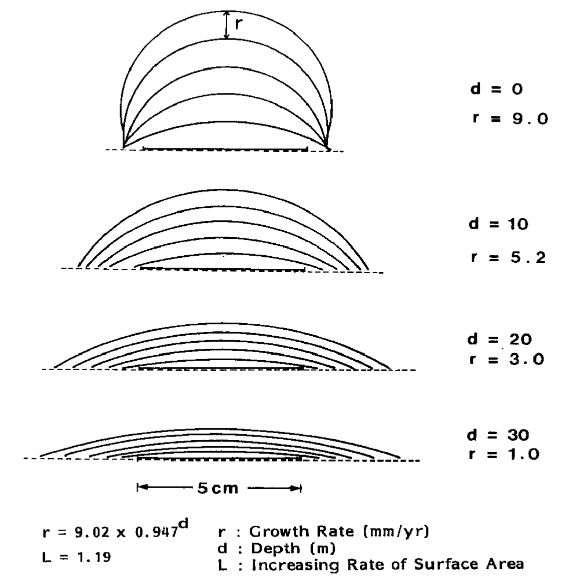


Fig. 25. Simulation depictions of growth form of *Porites australiensis* at depths 0, 10, 20 and 30 m. Dotted line indicates substratum.

$$r\,(\mathrm{mm}) = 9.02 \times 0.947^{d}$$

where d is depth (m). This function is a regression expression at St. 4 (Fig. 20). The specimens at St. 4 were chosen for the analysis, because they were collected through wider depth ranges in the reef than in the other stations.

On the other hand, the soft tissue thinly covers the surface of a corallum. So, the increasing rate of surface area is equal to the increasing rate of the volume of the soft tissue. The volume of the soft tissue is thought to be the function of nothing but the nutrients which are taken from the outside of corals (Graus and MacIntyre, 1976). If the distribution of the nutrients in a reef is regarded as constant, then the increasing rate of the soft tissue, or the increasing rate of the surface area will have a fixed value regardless of depth. The measurements of the *P. australiensis* specimens at St. 4 support this idea (Fig. 22). In the simulation, the average value of the increasing rate of the surface area of *P. australiensis* at St. 4 ($L = 1.19$) was adopted.

The simulation was carried out on the vertical plane so as to depict the vertical section of the corallum (Fig. 25). The surface outline of the corallum was supposed to be an arc shape, because the pressure of the skeletal growth is thought to be hydrostatical. During the skeletal growth, the margins of the surface attach to the substratum (lower three drawings of Fig. 25) or rest on the skeleton formed earlier (top drawing of Fig. 25). The simulation started from the five centimeters line because the growth form of *P.* spp. in any environments is laminar, till its diameter reaches a few centimeters.

The results of simulation are shown in Figure 25. Concentric curves indicate the annual rings equivalent to the density bands. The picture in 0 m in depth has a spherical shape. The shape of coralla is hemispherical at depths of 10 and 20 m, and becomes encrusting at a depth of 30 m. This result agrees well with the examples (Plate 27).

II. Pleistocene Corals

1. General Outline of the Study Area

Fossil corals and stratigraphy of the Ryukyu Group were investigated in Haterum-jima, Miyako-jima, Okinawa, Okierabu-jima and Kikai-jima (Fig. 1, Table 1). Among them, Okinawa includes three districts, namely, the southern part of Okinawa, Yomitan district and Katsuren Peninsula (Fig. 33).

The Ryukyu Group studied here is entirely of Pleistocene age.

There were many phases of transgressions and regressions in the middle Pleistocene (Chappell, 1974 ; Kikuchi, 1977). The climate of the Ryukyu Islands when the main part of the Ryukyu Group were deposited is thought to be similar to that of the present time, because the latitudinal range of the distribution of the Ryukyu Group is almost the same as that of Recent coral reefs. Through the present study, it became clear that the coral communities of the Ryukyu Group can be correlated to those of Recent coral reefs. The fact also supports the similarity of the climate.

Two types of the basement of the Ryukyu Group are recognized in the study areas. One is the Shimajiri Group which consists of weakly consolidated siltstone and sandstone. The other belongs to Cretaceous and Paleogene slates, sandstones and volcanics. The Ryukyu Group in Hateruma-jima, Miyako-jima, southern part of Okinawa and Kikai-jima lies on the Shimajiri Group, while the Group in the Yomitan district and Okierabu-jima overlies the Cretaceous basement, and that of the Katsuren Peninsula district occurs in the area where both types of the basements can be seen.

2. Methods

(1) Stratigraphy

Stratigraphy of the seven areas was studied in order to reconstruct the depositional environment of the Ryukyu Group. Field survey was carried out in Hateruma-jima, Okinawa and Kikai-jima. The stratigraphy of the Ryukyu Group in Miyako-jima and Okierabu-jima is discussed based on the data by Nakamori (1982) and Iryu (1983 MS), respectively.

The ages of the formations of the Ryukyu Group are discussed on the basis of radiometric dating and nannoplankton fossils. Radiometric ages of the Ryukyu Group in Hateruma-jima, Okinawa, Okierabu-jima and Kikai-jima are referred. They were measured by U-Th dating method and ESR (electron spin resonance) method previously (Konishi *et al.*, 1970; Konishi *et al.*, 1974; Konishi, 1980; Koba and Nakata, 1981; Omura, 1983, 1984; Kizaki *et al.*, 1984). Nannoplankton fossils were detected from the Ryukyu Group in Miyako-jima, Okinawa and Okierabu-jima.

(2) Fossil Coral Community

The community structures of fossil corals in the Ryukyu Group were studied in Hateruma-jima, Miyako-jima, southern part of Okinawa, Yomitan district of Okinawa, Okierabu-jima and Kikai-jima. The ecological data were based on the sketches depicted in the field.

A transparent vinyl plastic sheet on which meshes are drawn was used for the sketch. Width and height of the mesh are both one meter and intervals of meshes are ten centimeters. The vinyl plastic sheet was directly put on vertical outcrops, and corals and calcareous algae projected on it were sketched. Sketched corals were identified in the field. Some of the identifications were in the generic level, because of their poor preservation. Well-preserved samples were collected for photographing. The growth rates of the specimens belonging to the genus *Porites* were measured on the top of the coralla.

The number of sketches is 8 in Hateruma-jima, 27 in Miyako-jima, 24 in the southern part of Okinawa, 22 in Yomitan district, 29 in Okierabu-jima and 10 in Kikai-jima. Areas of the sketches in one locality range from 0.8 to 6 m^2, about 1.8 m^2 on average.

The covered areas of each coral taxonomic group in every sketch were calculated with NEC PC 9800 Series computer. The ratio of the areas covered by corals belonging to a certain taxon in the total sketched area was computed in each sketch and in each study district. Pielou's equitability index (J') in each locality was also computed from the ratio of each taxonomic group. Several coral communities were recognized based on these ecological features and sedimentary structures of the sketched areas. Paleoenvironments in which they lived were estimated by the correlation to the Recent communities. Paleogeographic maps of each area were drawn based on the paleoenvironmental

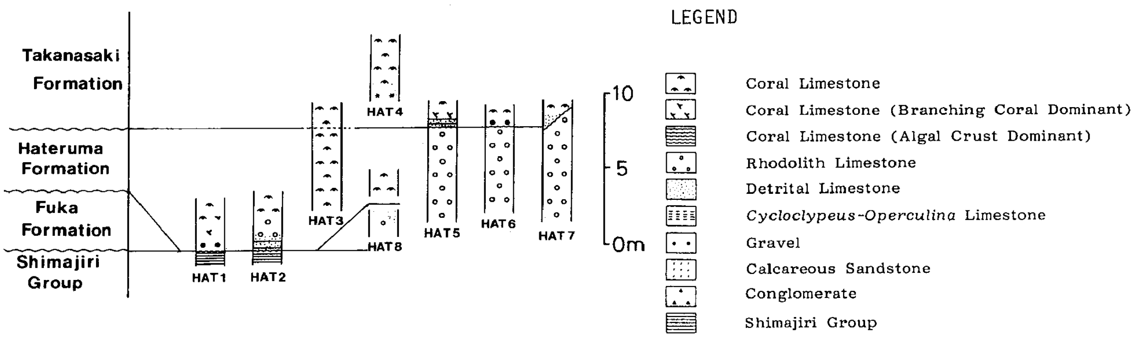


Fig. 26. Columnar sections of the Ryukyu Group in Hateruma-jima.

Table 7. Generalized stratigraphic succession of Hateruma-jima.

Geologic Age	Formation		Thickness	Sediments
Holocene	Beach, Alluvial & Reef Deposits			Sand, Gravel, Clay & Limestone
Pleistocene	Ryukyu Group	Takanasaki Formation	~15m	Coral Limestone; Detrital Limestone
		Hateruma Formation	5~25m	Coral Limestone; Rhodolith Limestone; Detrital Limestone; COL.
		Fuka Formation	~20m	Detrital Limestone
Pliocene	Shimajiri Group			Siltstone & Sandstone

COL.: *Cycloclypeus-Operculina* Limestone

data from the corals, rhodoliths and larger foraminifers.

3. Results

(1) Stratigraphy

a. Hateruma-jima

Okimura (1978) studied the stratigraphic sequences of Hateruma-jima and divided them into the Shimajiri Group (Pliocene), A, B and C Formations of the Ryukyu Group (Pleistocene), Raised Coral Reef and Recent deposits (Holocene) in ascending order.

The same stratigraphic sequences are recognized in this study. Okimura (*op. cit.*) did not give the formation names based on the general customs of nomenclature to the strata of the Ryukyu Group, so, A, B and C Formations are here renamed Fuka, Hateruma and Takanasaki Formations, respectively. The coral limestone which Okimura (1978) and Kawana and Oshiro (1978) considered to be the Raised Coral reef is of Pleistocene age by U-Th dating (Konishi, 1980: Kizaki *et al.*, 1984; Omura, 1983, 1984).

The stratigraphic sequences of Hateruma-jima are shown in Table 7. Geological map and columnar sections are shown in Figs. 26 and 27.

In the previous studies, the name "algal ball limestone" was used for limestone containing "algal balls" (Minoura, 1979; Minoura and Nakamori, 1982; Nakamori *et al.*, 1981; Nakamori, 1982). But "rhodolith limestone" is adopted in this study, because "rhodolith" was proposed for the algal ball composed of the skeletons of Rhodophyta (Barnes *et al.*, 1970; Ginsburg and Bosellini, 1973). I used "larger foraminiferal limestone" in the foregoing study for limestone in which the larger foraminifers, *Cycloclypeus* and *Operculina*, predominate (Nakamori, 1982). But, it is here renamed "*Cycloclypeus-Operculina* limestone", since the larger foraminifers besides the genera *Cycloclypeus* and *Operculina* are contained in almost all

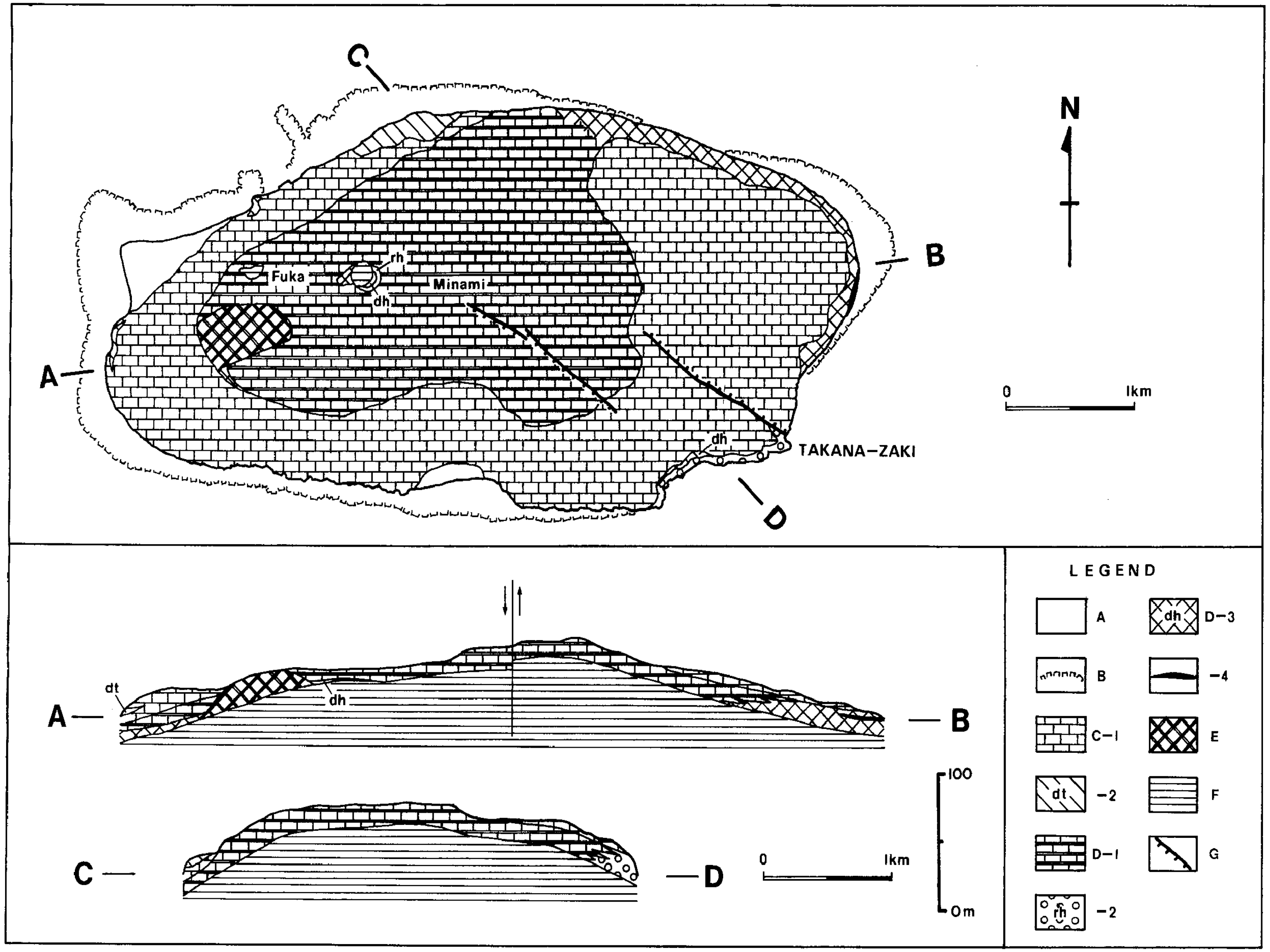


Fig. 27. Geological map of Hateruma-jima for the Ryukyu Group.
A : Recent beach and alluvial deposits ; B : Recent coral reefs ; C : Takanasaki Formation ; C-1 : Coral limestone ; C-2 : Detrital limestone ; D : Hateruma Formation ; D-1 : Coral limestone : D-2 ; Rhodolith limestone ; D-3 : Detrital limestone ; D-4 : *Cycloclypeus-Operculina* limestone ; E : Fuka Formation : F : Shimajiri Group ; G : Fault.

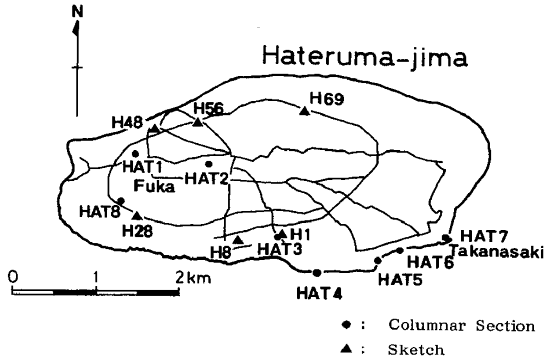


Fig. 28. Map showing localities of columnar sections and sketches of fossil coral communties in Hateruma-jima.

the limestones in the Ryukyu Group.

1) Fuka Formation

The Fuka Formation has its type locality at the cutting, south to Fuka hamlet in the western part of the island. Type section HAT8 is shown in Fig. 26. The formation occurs on the western part of the Terrace 1 of Ota *et al.* (1982) and outcrops in a narrow area. It consists of massive detrital limestone with rhodoliths. The limestone is well consolidated and has dark red color. The thickness of the Fuka Formation is believed to be less than 20 m. The Formation lies on the Shimajiri Group unconformably.

2) Hateruma Formation

The Hateruma Formation composes the Terrace 1 of Ota *et al.* (*op. cit.*). It outcrops in the middle part of the island and along the coast excluding the western part of the island. The type locality is situated at the quarry, south to Hateruma hamlet in the middle part of the island. Its type section HAT2 is shown in Fig. 26. The Hateruma Formation is well exposed at the Takana Cape in the southeastern end of the island. Its section is shown in the lower part of HAT7 in Fig. 26. The Hateruma Formation is composed of coral limestone in the middle, detrital limestone in the western and rhodolith limestone in the southern parts of the island. The coral limestone contains numerous branching corals in the northern half of Hateruma-jima. The detrital limestone intercalates *Cycloclypeus-Operculina* limestone in places. The Hateruma Formation is 5–25 m in thickness and overlies the Shimajiri Group unconformably. The boundary between them is observed in the quarry, west to Fuka hamlet and the type locality. The relation of the Fuka and Hateruma Formations is thought to be an unconformity, because gravels of the Fuka Formation are contained in the Hateruma Formation.

Many U-Th datings have been carried out and indicate that the age of the Hateruma Formation is 200,000 to 300,000 yr BP (Kawana and Oshiro, 1978; Konishi 1980; Ota *et al.*, 1982; Omura, 1983, 1984; Kizaki *et al.*, 1984).

3) Takanasaki Formation

The Takanasaki Formation has its type locality at the Takana Cape in the southern part of the island. Its section is shown in the upper part of HAT7 in Fig. 26. It is distributed along the Terrace 3 of Ota *et al.* (1982), that is to say, the margin of the island. The Takanasaki Formation consists of coral limestone intercalated with detrital limestone. The coral limestone which contains a lot of branching corals occurs in the northern part of the island. The limestone is weakly consolidated and the state of preservation of fossil corals is fairly good. The relation between the Takanasaki Formation and the Hateruma Formation is unconformable and can be observed along the cliff in the western and southern parts of the island.

Konishi (1980) and Omura (1983, 1984) reported that the radiometric age of the Takanasaki Formation is 130,000 y BP.

b. Miyako-jima

There are two different opinions on the stratigraphy of the Ryukyu Group developed in Miyako-jima. One insists that the Ryukyu Group in Miyako-jima can

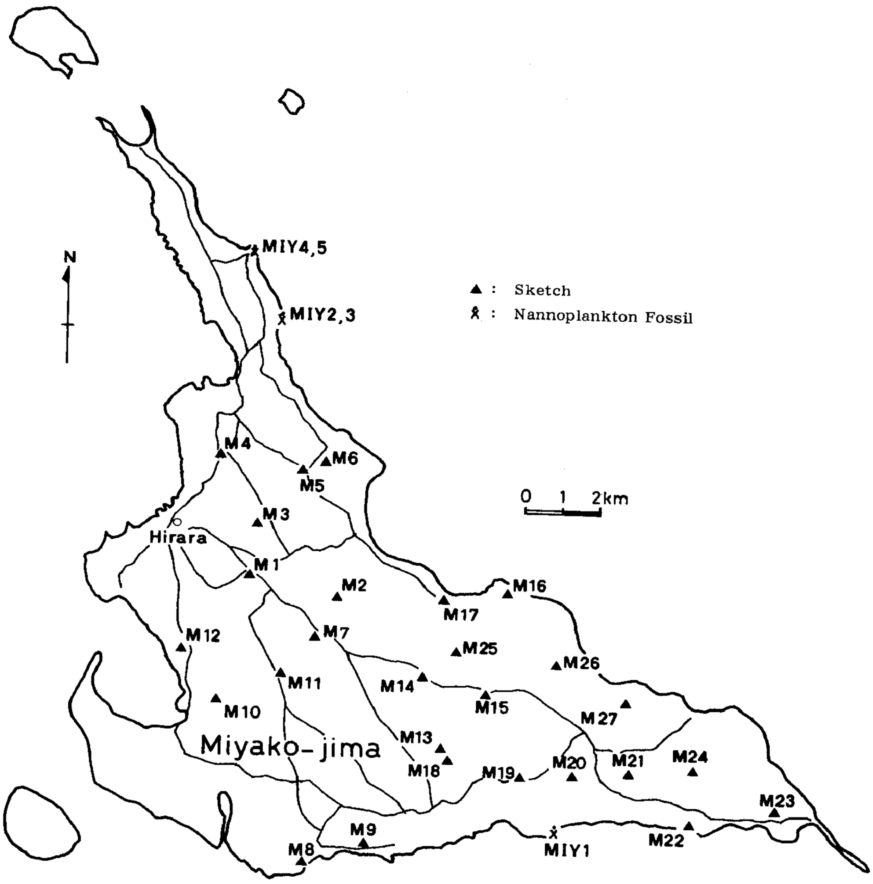


Fig. 29. Map showing sampling sites of nannoplankton fossils and localities of sketches of fossil coral communities in Miyako-jima.

be divided into many strata lying one upon another unconformably (Doan *et al.*, 1960; Omura, 1973; Yazaki, 1976, 1978; Yazaki and Oyama, 1979, 1980). The other is that the Ryukyu Group is composed of continuous sequences without any stratigraphic breaks in the main part of Miyako-jima (Okinawa Quaternary Research Group, 1976; Furukawa, 1975; Furukawa *et al.*, 1979; Kameyama and Shuto, 1980; Nakamori, 1982). In this study, the stratigraphy proposed by Nakamori (1982) is adopted.

The Ryukyu Group in Miyako-jima is composed of the Miyako-jima and the Shimoji-jima Limestones in ascending order. The former occurs in almost all the part of Miyako-jima, while the latter is restricted only in Shimoji-jima and overlies the former unconformably. Three sedimentary cycles, each of which

Table 8. List of nannoplankton fossils in Miyako-jima and Okinawa.

	Miyako-jima					Okinawa									
	MIY 1	MIY 2	MIY 3	MIY 4	MIY 5	OKI 1	OKI 2	OKI 3	OKI 4	OKI 5	OKI 6	OKI 7	OKI 8	OKI 9	OKI 10
Calcidiscus leptoporus			+			+	+								
Crenalithus doronicoides			+	+	+	+	+								+
Cyclolithella annula										+		+	+		
Discoaster brouweri				+											
D. surculus		+					+								
Emiliania huxleyi	+														
Gephyrocapsa caribbeanica			+			+	+	+			+	+		+	
G. oceanica	+	+	+			+	+	+	+	+	+	+	+	+	+
G. cf. protohuxleyi											+				
Helicopontosphaera sellii								+							
H. wallichi												+			
Helicosphaera carteri						+									
Pseudoemiliania lacunosa						+	+	+							
P. pacifica								+	+		+	+			
Rhabdosphaera claviger									+		+		+		
Reticulofenestra pseudoumbilica		+	+					+	+	+	+	+	+		
Sphenolithus abies							+								
Umbilicosphaera sp.			+						+	+	+				

begins with *Cycloclypeus-Operculina* limestone or detrital limestone, and ends in coral limestone, were recognized in the Miyako-jima Limestone. They are named the Lower, the Middle and the Upper Parts (Nakamori, *op. cit.*).

The geologic age of the Ryukyu Group

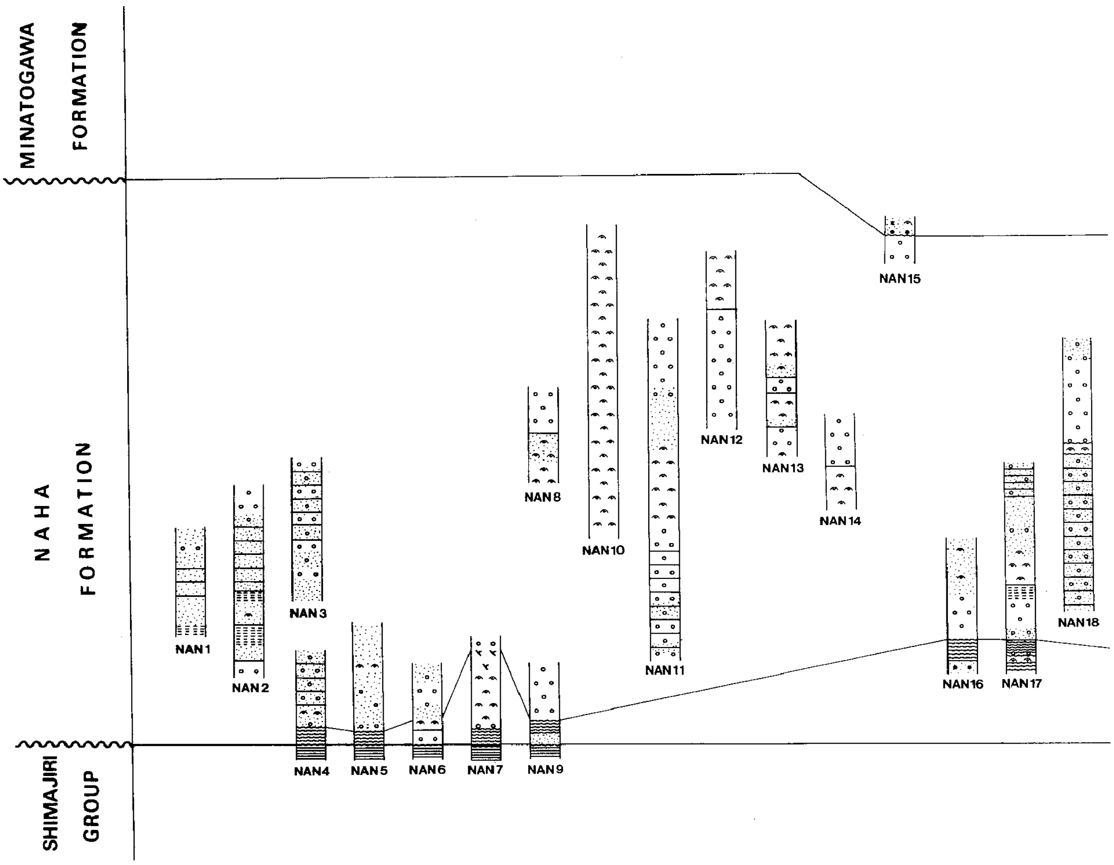
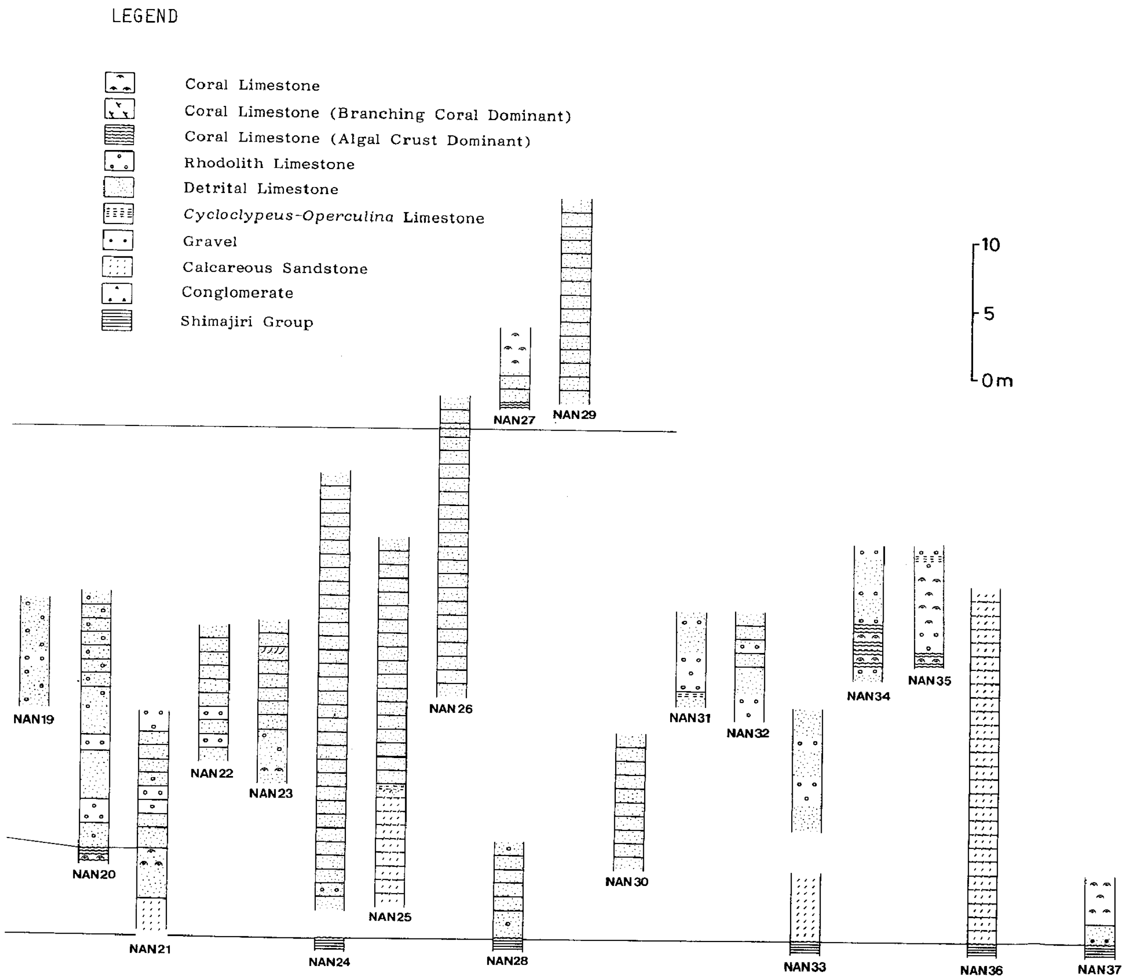


Fig. 30. Columnar sections of the Ryukyu

in Miyako-jima has hitherto remained uncertain, because the larger foraminiferal biostratigraphy in the Pleistocene has not been established and reliable radiometric ages of the Miyako-jima Limestone have not been reported. However, new biostratigraphic data were added by discovery of nannoplankton fossils in the present study. The fossils were found from the Lower Part of the Miyako-jima Limestone, which is characterized by *Cycloclypeus* and *Operculina* (Fig. 29: See also columnar sections nos. 4 and 43 in Nakamori, 1982, Fig. 4). Nannoplankton species obtained are listed in Table 8. It is remarkable that *Emiliania huxleyi* is contained in MIY1. Since the age of the first appearence of *E. huxleyi* is 270,000 yr BP (Haq and Takayama, 1984), the Miyako-jima Limestone is to be younger than 270,000 years. The Shimoji-jima Limestone can be correlated to the Takanasaki Formation in Hateruma-jima, owing to its altitude and the degree of consolidation.

c. Okinawa

Flint *et al.* (1959) divided the Ryukyu Group in Okinawa into four formations. They are the Naha Formation, the Kunchan Gravel, the Yontan Limestone and the Machinato Limestone in ascending order. Flint *et al.* (*op. cit.*) noted that the relations among the formations are all unconformable. Many studies



Group in the southern part of Okinawa.

Table 9. Generalized stratigraphic succession of the Ryukyu Group in Okinawa.

Geologic Age	Formation		Thickness	Sediments
Holocene	Beach, Alluvial & Reef Deposits			Sand, Gravel, Clay & Limestone
Pleistocene	Ryukyu Group	Minatogawa Formation	~15m	Detrital Limestone; Coral Limestone
		Naha Formation	5~50m	Detrital Limestone; COL.; COL.; Rhodolith Limestone; Coral Limestone; Cgl.; CS.
Pre-Pleistocene	Shimajiri Group			Siltstone, Sandstone & Tuff
	Inogama Formation			Sandstone & Slate
	Miyagi Formation			

COL. : *Cycloclypeus-Operculina* Limestone
CS. : Calcareous Sandstone
Cgl. : Conglomerate

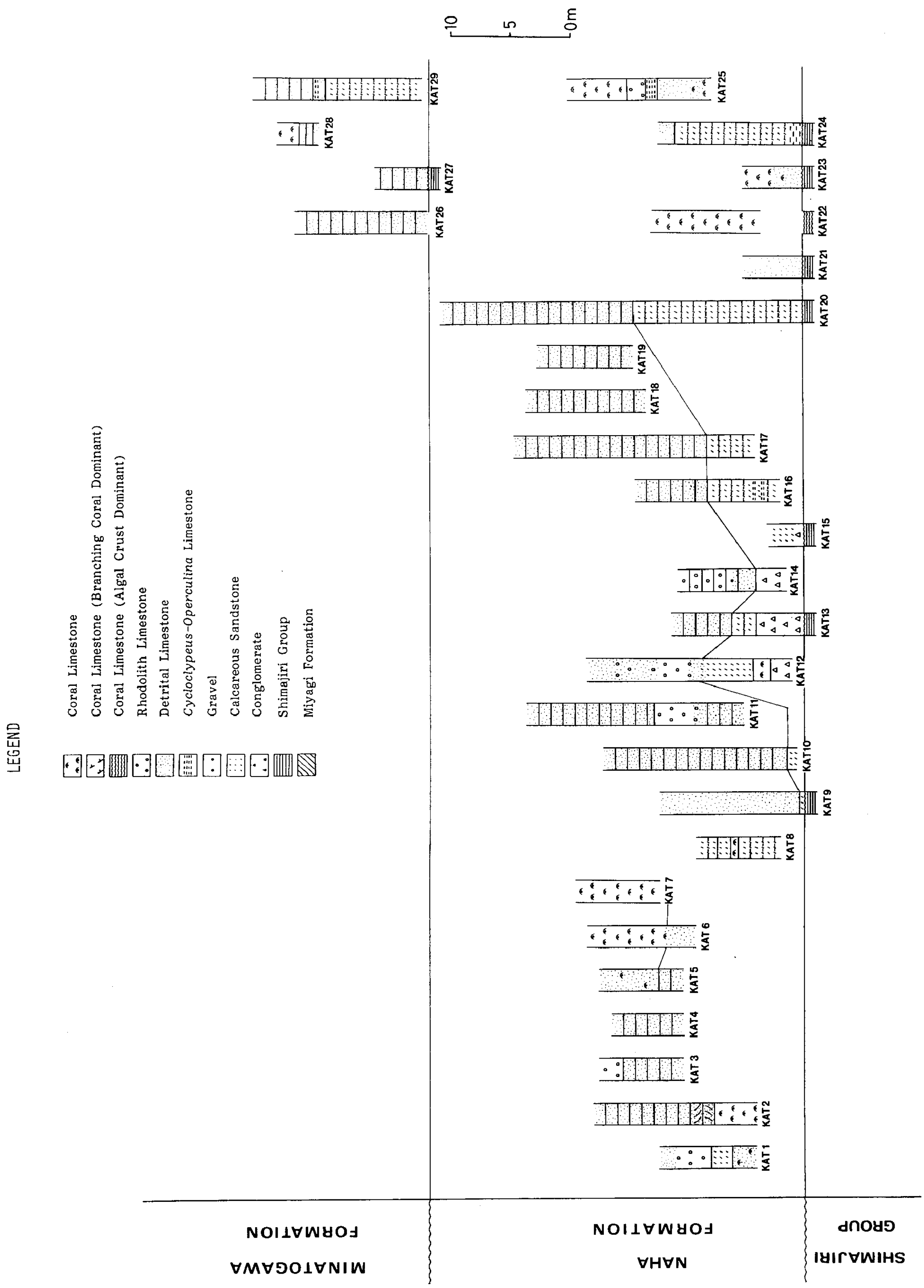


Fig. 31. Columnar sections of the Ryukyu Group in the Katsuren Peninsula district.

after them indicate similar ideas (MacNeil, 1960 ; Shoji, 1968 ; Okinawa Quaternary Research Group, 1976 ; Okimura *et al.*, 1977 ; Koba, 1980). Takayasu (1978) divided the Pleistocene formations in Okinawa into "accessory limestone" and "main limestone", and mentioned that the Naha Formation and Yontan Limestone should be contained in the "main limestone" together. He mentioned that the relation of the formations is partly unconformable. Furukawa (1979) mentioned that a distinct unconformity is not recognized between them.

1) Naha Formation

The Kunchan Gravel, the Naha Formation and the Yontan Limestone are unified together and called them the Naha Formation here, because they cannot be divided into different stratigraphic units owing to the following reasons.

The gravel, detrital limestone with rhodolith and coral limestone which constitute the high terrace was named the Kunchan Gravel, Naha Formation and Yontan Formation, respectively (Flint *et al.*, 1959). Flint *et al.* (*op. cit.*) thought that the Naha Formation is the lowest and the Yontan Formation is the uppermost in the stratigraphic sequence of the Ryukyu Group. However, it became clear that these limestones and gravels indicate contemporaneous heterotopic facies and each limestone or gravel appears repeatedly in various horizons in several sections.

The Naha Formation has its type locality at the quarry between Yaese-dake and Yoza-dake in the southern part of Okinawa. The type section is shown by NAN11 in Fig. 30. A section at the quarry in the south of Takashiho, Yomitan Village is also referred to because the Formation can be observed thoroughly. Its section is shown by YON8 in Fig. 32.

Gravels of the Naha Formation occur mainly in the eastern part of the Yomitan district and the northeastern part of the Katsuren Peninsula district, where the basement of the Ryukyu Group is Cretaceous slate and sandstone. They are contemporaneous with the limestones of the Naha Formation, and range from the lowest to uppermost part of the Formation. The gravels are unconsolidated and accompanied by plant fragments in places.

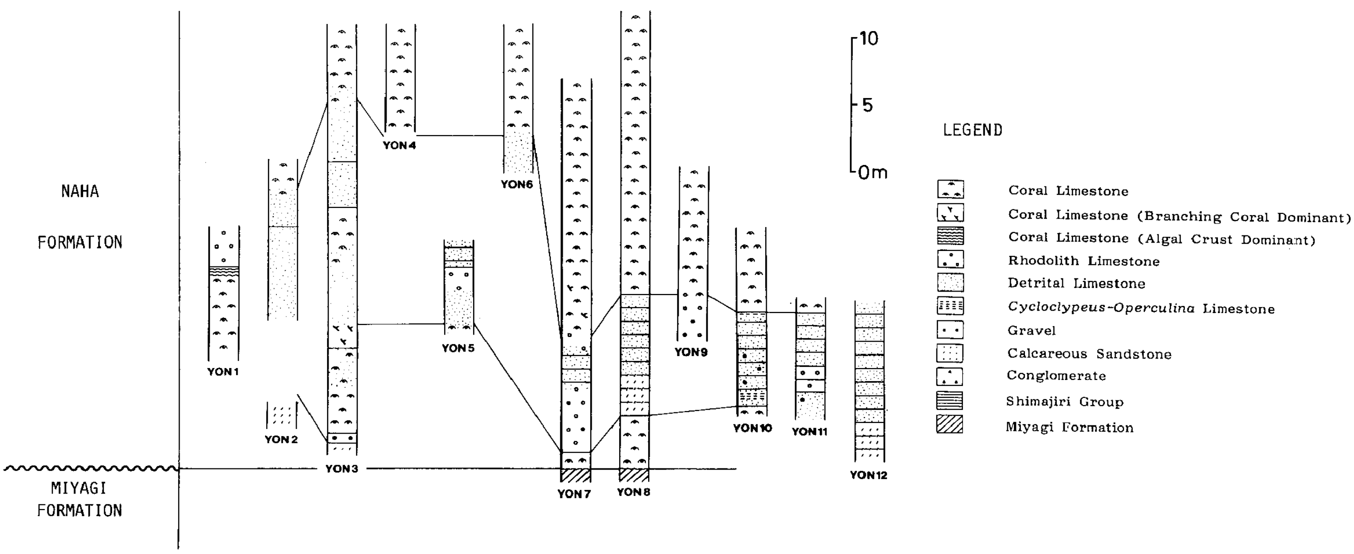


Fig. 32. Columnar sections of the Ryukyu Group in the Yomitan district.

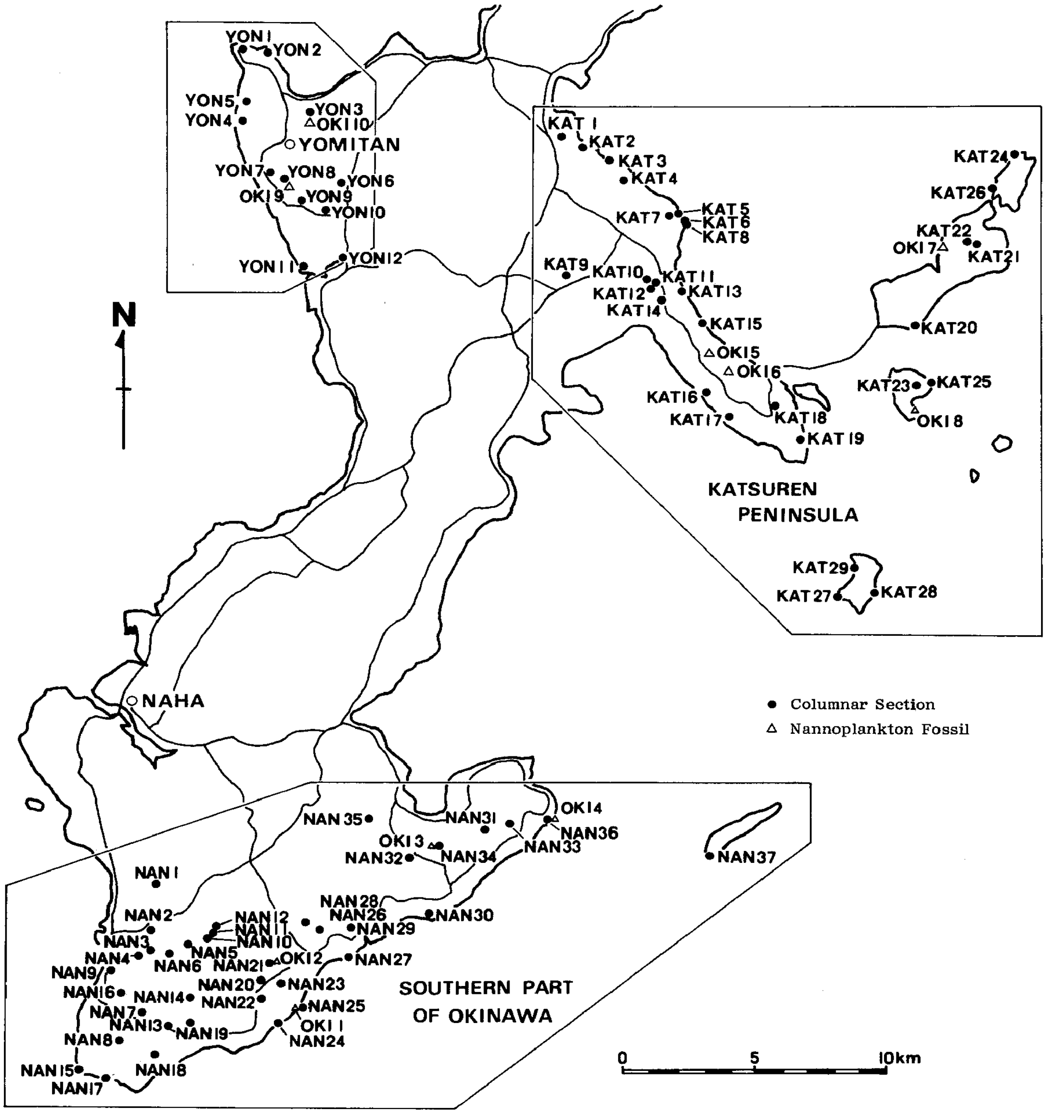


Fig. 33. Map showing localities of columnar sections and sampling sites of nannoplankton fossils in Okinawa.

Brown colored calcareous sandstone is developed around Mabuni and Chinen in the southern part of Okinawa, around Uchima in the Katsuren Peninsula, Hamahiga-jima, Henza-jima and Miyagi-jima. It frequently occurs in the lowest part of the Naha Formation and overlies the Simajiri Group unconformably. The calcareous sandstone is weakly consolidated and yields the tests of larger foraminifers, molluscs and brachiopods.

Coral limestone is mainly found in the lowest and the uppermost parts of the Naha Formation. It excels especially around Ihara, Yozadake and Oyakebaru in the southern part of Okinawa, in Henza-jima, Miyagi-jima and Hamahiga-jima in the Katsuren Peninsula district, and around Yomitan Air Port. The coral limestone in the lowest part contains thick algal crusts.

Rhodolith limestone occurs so as to surround the area in which the coral limestone is mainly distributed. It is contemporaneous with the coral limestone and interfingers with it. Rhodolith limestone scarcely occurs in the Katsuren Peninsula district.

Detrital limestone was deposited contemporaneously with the coral and rhodolith limestones and is distributed around them in the southern part of Okinawa and Yomitan district. It also develops in the Katsuren Peninsula. The detrital limestone is well-stratified and inclines southeastward in the Katsuren Peninsula, and toward the center of the distribution area of the detrital limestone in Minatogawa. Its facies changes gradually into the rhodolith limestone toward the distribution center of the coral limestone.

Cycloclypeus-Operculina limestone is intercalated in or found under the detrital limestone. Its thickness is less than 2 m. The limestone is observed in Itokazu, Kakazu, Kuniyoshi and Nashiro in the southern part of Okinawa, Uchima in the Katsuren Peninsula and Oki in the Yomitan district. Most grains of the limestone consist of the tests of *Cycloclypeus* and *Operculina*.

Generalized relationship among the gravel and limestones is shown in Table 9. The Naha Formation overlies the Shimajiri Group or Cretaceous sandstone and slate unconformably. It is 50 m in the maximum thickness.

Kizaki *et al*. (1984) reported the radiometric age of the fossil coral in the Ryukyu Group in the Katsuren Peninsula district. He mentioned that it is older than 300,000 yr BP.

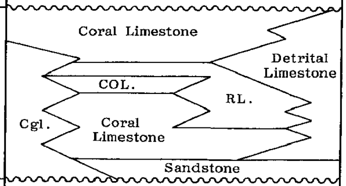
Nannoplankton fossils were obtained from the calcareous sandstones in the lowest part of the Naha Formation in the southern part of Okinawa and the Katsuren Peninsula district (Fig. 33, Table 8). *Gephyrocapsa* spp., *Helicopontosphaera sellii*, *Pseudoemiliania lacunosa*, *P. pacifica* and *Discoaster* spp. were recognized in them. But, *H. sellii*, *P. lacunosa*, *P. pacifica* and *Discoaster* spp. are considered to be derived fossils from the Shimajiri Group. The nannoplankton fossils were also found out from the calcareous sandstone between the coral and detrital limestone in the Yomitan district (YON8 in Fig. 32). *Gephyrocapsa* spp. were obtained, and *P. lacunosa* and *P. pacifica* were not observed. On the other hand, *Emiliania huxleyi* was not found from the Ryukyu Group in Okinawa. Consequently, the nannoplankton fossils in the Ryukyu Group of Okinawa are considered to belong the zone NN20 of Martini (1971). The age of the zone ranges from 460,000 to 270, 000 yr BP (Haq and Takayama, 1984). It agrees well with the radiometric age mentioned above.

2) Minatogawa Formation

Poorly consolidated limestones which outcrop along the west coast of the southern part of Okinawa and in the islets are called the Minatogawa Limestone by Takayasu (1976, 1978). In the present study, the name Minatogawa Formation is adopted, because the limestones are associated with calcareous sandstones at Tsuken-jima.

The Minatogawa Formation has its type locality at the quarry of Minatogawa in the southern part of Okinawa (Takayasu, 1976). Its section is shown by NAN29 in Fig. 30. The Formation constitutes terraces whose height ranges from 0 to 50 m, and consists of detrital limestone and coral limestone. The detrital limestone is well stratified and grain-supported sedimentary structure which makes the appearance of the limestone porous. It is distributed at Kyan Cape, around Minatogawa and Gushiken in the southern part of Okinawa and in Ikei-jima in the Katsuren Peninsula district. The coral limestone of the Minatogawa Formation is more porous and less consolidated than that of the Naha Formation. It occurs in Kudaka-jima, along the coast of Minatogawa and in Tsuken-jima. The thickness of the Minatogawa Formation is at most 20 m and overlies the Naha Formation or the Shimajiri Group unconformably. The relationship between the limestones and

Table 10. Generalized stratigraphic succession of the Ryukyu Group in Okierabu-jima (Compiled from Iryu, 1983 MS).

Geologic Age	Formation		Thickness	Sediments
Holocene	Beach, Alluvial & Reef Deposits			Sand, Gravel, Clay & Limestone
Pleistocene	Ryukyu Group	Okierabujima Formation	~ 90m	
Pre-Tertiary	Neori Formation			Sandstone, Slate, Basalt & Granodiorite

COL.: *Cycloclypeus-Operculina* Limestone
RL. : Rhodolith Limestone
Cgl. : Conglomerate

sandstone of the Minatogawa Formation is shown in Table 9.

The Minatogawa Formation can be correlated to the Takanasaki Formation in Hateruma-jima based on the degree of consolidation and the altitude of the terraces.

Geological maps of the Ryukyu Group in Okinawa are shown in Figs. 34, 35 and 36.

d. Okierabu-jima

Nakagawa (1967) divided the Ryukyu Group in Okierabu-jima into the Shimoshiro, Sinjo and Serikaku Formations in ascending order. Their relations were thought to be unconformable. Minoura (1979) followed the stratigraphy proposed by Nakagawa (*op. cit.*). On the other hand, the idea that the main part of the Ryukyu Group in Okierabu-jima consists of a continuous sequence has been proposed (Koba, 1980; Iryu, 1983 MS; Noda, 1984a, b). Since no unconformities were confirmed in this study, the name Okierabu-jima Formation proposed by Iryu (*op. cit.*) is adopted for the Ryukyu Group in Okierabu-jima.

The type locality of the Okierabu-jima Formation is situated in the area from China, China Town to O-yama in the central part of Okierabu-jima (Iryu, *op. cit.*). The Formation covers most parts of Okierabu-jima except for the summits of O-yama and Shiro-yama. Generally speaking, conglomerate, coral limestone, rhodolith limestone and detrital limestone occur concentrically from inward to outward around O-yama, where the basement rocks of the Ryukyu Group outcrop; those are contemporaneous and interfinger each other. Sandstone and siltstone are frequently intercalated in the conglomerate. Thin beds of calcareous sandstone and conglomerate are observed in the limestone in places. A pair of *Cycloclypeus-Operculina* limestone and rhodolith limestone beds is intercalated in the coral limestone along the 150 m contour in altitude. The coral limestone in Okierabu-jima contains more calcareous algae than that of Hateruma-jima, Miyako-jima and Okinawa.

The relation of each facies is shown in Table 10. The thickness of the Okierabu-jima Formation reaches 100 m. The Formation overlies the Jurassic-Cretaceous Neori Formation unconformably.

The geological map of Okierabu-jima is shown in Fig. 37.

Radiometric ages by ^{230}Th and ^{231}Pa methods of the Ryukyu Group at Kunigami Cape in the northern end of Okierabu-jima range from 79,000 to 99,500 yr BP (Konish *et al.*, 1970; Konishi *et al.*, 1974). Koba and Nakata (1981) reported ESR ages from 313,000 to

Table 11. Generalized stratigraphic succession of the Ryukyu Group in Kikai-jima.

Geologic Age	Formation		Thickness	Sediments
Holocene	Beach, Alluvial & Reef Deposits			Limestone, Gravel, Sand & Clay
Pleistocene	Ryukyu Group	Wan Formation	~20m	Coral Limestone; Rhodolith Limestone; Detrital Limestone
		Takigawa Formation	~15m	Coral Limestone
		Hyakunodai Formation	~25m	Rhodolith Limestone; Detrital Limestone
Pliocene	Shimajiri Group			Siltstone & Sandstone

625,000 yr BP at the same point mentioned above and the age from 320,000 to 160,000 yr BP near O-yama. The difference between radiometric and ESR ages at Kunigami Cape is thought to be due to the excess from the confidence range of radiometric method. Nannoplankton fossils were obtained from the calcareous sandstone at Wanjo-hama along the north coast of Okierabu-jima. *Gephyrocapsa oceanica* was obtained, but *Pseudoemiliania lacunosa* and *Emiliania huxleyi* were not recognized (Iryu, 1983 MS). The horizon yielding the nannoplankton fossils is correlated to the zone 20 of Martini (1971) which ranges from 460,000 to 270,000 yr BP. Consequently, the age of the Okierabu-jima Formation is thought to be the middle Pleistocene.

e. Kikai-jima

The Ryukyu Group in Kikai-jima was divided into the Hyakunodai and Wan Formations in ascending order (Nakagawa, 1969; Minoura, 1979). In this study, two lithostratigraphic units whose relation is unconformity were discriminated in the Hyakunodai Formation in the sense of Nakagawa. The lower stratum is here called the Hyakunodai Formation and the upper the Takigawa Formation. The same name "Hyakunodai Formation" is used, because the Formation here defined occupies the most part of the Hyakunodai Formation previously used (Table 11).

1) Hyakunodai Formation

The Hyakunodai Formation is found in the Hyakunodai in the central to eastern part of Kikai-jima and constitutes the terrace whose altitude ranges from 150 to 224 m. Its type locality is situated in Hyakunodai (Nakagawa, 1969). The Formation consists of detrital and rhodolith limestones. The detrital limestone occurs all over Hyakunodai. The rhodolith limestone occurs around Takigawa hamlet and the southern part of Hyakunodai, and overlies the detrital limestone. These limestones are well consolidated and tinted brown to dark red. The thickness of the Hyakunodai Formation is about 25 m. The Formation overlies the Shimajiri Formation unconformably.

2) Takigawa Formation

The Takigawa Formation has its type locality along the forest road which connects Takigawa and Oasato hamlet, and occurs mainly in the northern and southern parts of Hyakunodai. It consists of coral limestone which contains abundant algal crusts, and is 15 m in thickness. The relation between the Takigawa and Hyakunodai Formations is an unconformity, and is observed in outcrops along the road which runs through the summit of Hyakunodai.

3) Wan Formation

The Wan Formation constitutes the terrace which ranges from 10 to 80 m in altitude. It occurs in the northern part and the western half of Kikai-jima. Its

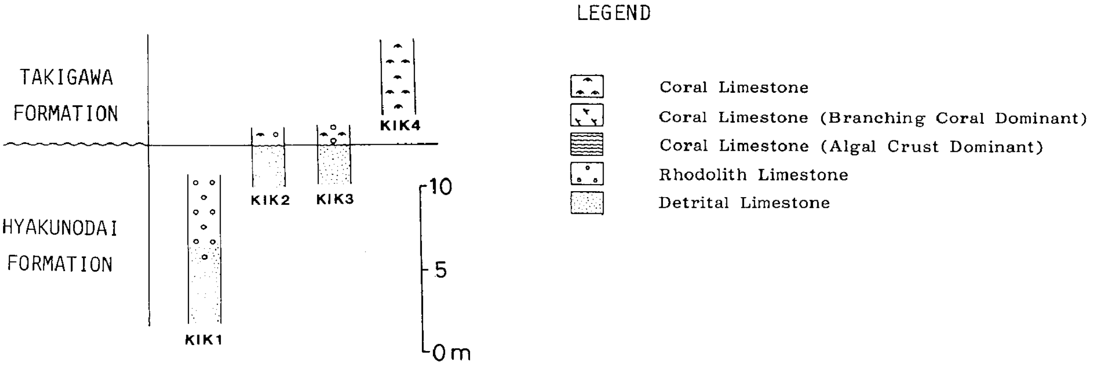


Fig. 38. Columnar sections of the Ryukyu Group in Kikai-jima.

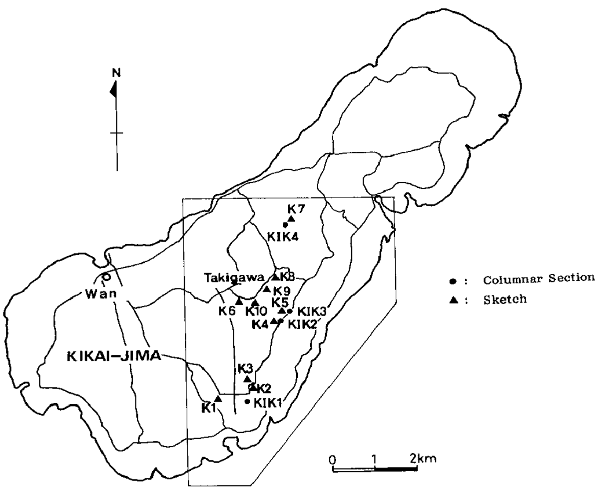


Fig. 39. Map showing localities of columnar sections and sketches of fossil coral communities in Kikai-jima.

type section is a cliff along the road in the vicinity of the Wan Elementary School, Wan hamlet. The Formation consists mainly of unconsolidated or weakly consolidated detrital limestone. Coral limestone is distributed sporadically in the western half of Kikai-jima. The preservation of fossil corals is fairly good. Rhodolith limestone occurs in places. The Formation overlies the Shimajiri Group with unconformity. Its thickness is about 20 m.

The stratigraphic sequence and the geological map of the Ryukyu Group in Kikai-jima are shown in Table 11 and Fig. 40, respectively.

Radiometric ages were reported from the Ryukyu Group in Kikai-jima and indicate that the base of the Hyakunodai Formation is older than 300,000 yr BP and the Takigawa Formation is 120,000 to 130,000 yr BP (Kizaki *et al.*, 1984; Konishi, 1967; Konishi *et al.*, 1970; Konishi *et al.*, 1974; Omura *et al.*, 1985). The age of the Wan Formation has been thought to range from 40,000 to 80,000 yr BP, but an age older than 300,000 yr was reported from the base of the Formation recently (Omura *et al.*, 1985).

f. Correlation

The Naha Formation, the lower part of the Okierabu-jima Formation and the Hyakunodai Formation are correlated with each other. Although the age of the Fuka Formation is unknown, it may be correlated to those formations mentioned above based on stratigraphic positions in the Ryukyu Group of Hateruma-jima and the extent of diagenesis.

The Hateruma Formation, the Miyako-jima Limestone and the upper part of the Okierabu-jima Formation are considered to be about 200,000 yr BP and can be correlated to the strata which constitute the terrace B IV in Barbados (Mesollella *et al.*, 1969).

The Takanasaki Formation, the Shimoji-jima Limestone, the Minatogawa Formation and the Takigawa Formation are about 130,000 yr BP and are correlated to the strata which make the Shimo-sueyoshi Surface and the terrace B III in Barbados (Kikuchi, 1977; Mesollella *et*

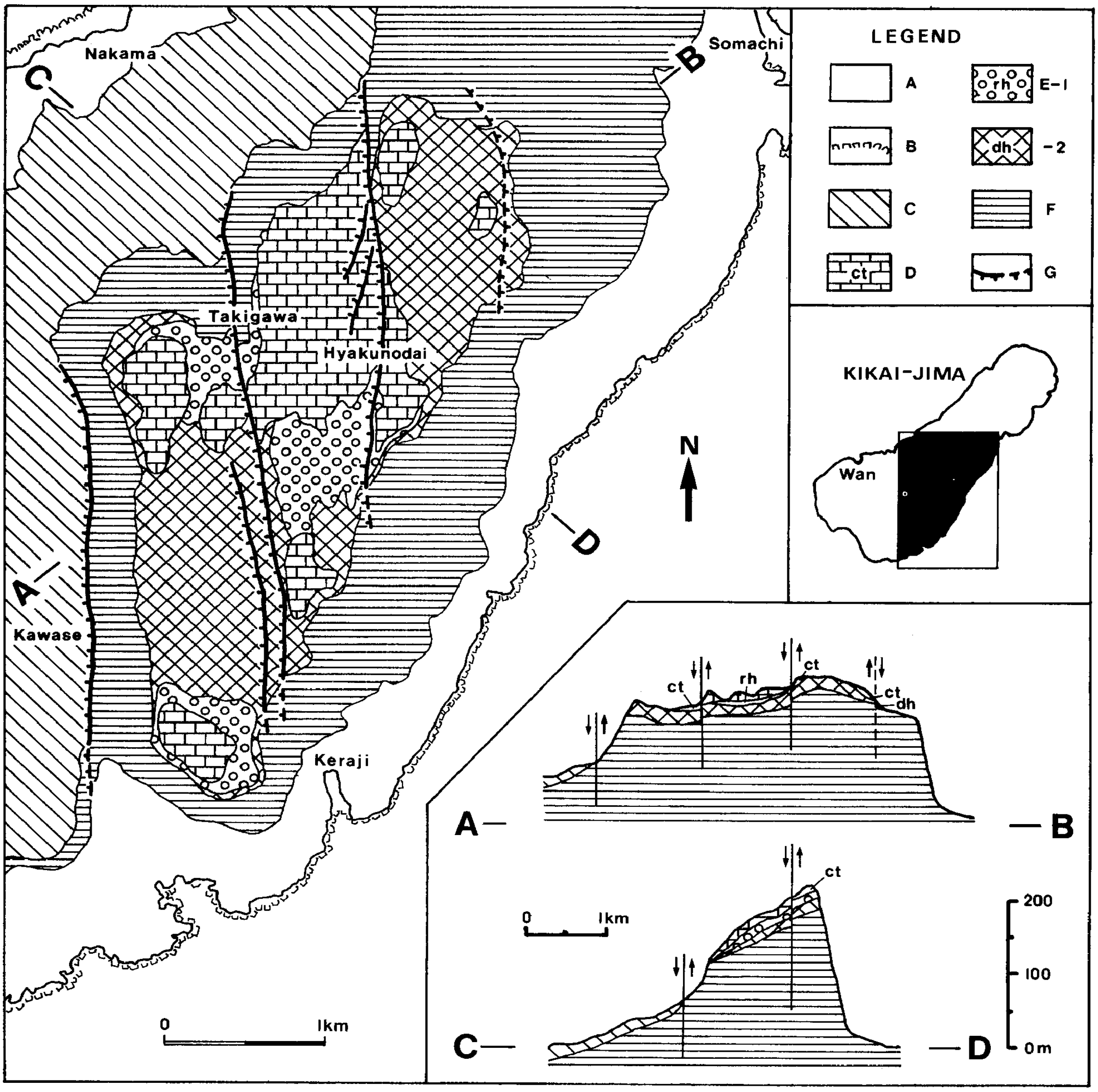


Fig. 40. Geological map of Kikai-jima for the Ryukyu Group.
A : Raised Coral reefs and Recent alluvial deposits ; B : Recent coral reefs ; C : Wan Formation ; D : Takigawa Formation ; E : Hyakunodai Formation ; E-1 : Rhodolith limestone ; E-2 : Detrital limestone ; F : Shimajiri Group ; G : Fault.

al., 1969).

The Wan Formation is younger than any other formations of the Ryukyu Group and cannot be correlated to other strata in this study.

These correlations are shown in Table 12.

(2) Community Structures

Ecological studies of the fossil corals were carried out in the Hateruma and Takanasaki Formations in Hateruma-jima, the Miyako-jima Limestone in Miyako-jima, the Naha Formation in Okinawa, the Okierabu-jima Formation in Okierabu-jima and the Takigawa Formation in Kikai-jima (Table 12, Figs. 28, 29, 39, 41, 42 and 43).

a. Diversity

Forty-eight genera and sixty-eight species of hermatypic scleractinian corals and two genera of ahermatypic scleractinian coral were recognized in this study. *Heliopora coerulea* and *Tubipora*

Table 12. Correlation table of the Ryukyu Group in six areas.

		Hateruma-jima	Miyako-jima (Nakamori, 1982)	Southern Part of Okinawa Katsuren	Yomitan	Okierabu-jima (Iryu, 1983 MS)	Kikai-jima	
Holocene		Beach and Alluvial Deposits	Beach and Alluvial Deposits	Beach and Alluvial Deposits Raised Coral Reef	Beach and Alluvial Deposits	Beach and Alluvial Deposits	Beach and Alluvial Deposits Raised Coral Reef	1
Late Pleistocene	Ryukyu Group						Wan Formation	
Middle Pleistocene		Takanasaki Formation	Shimojijima Limestone	Minatogawa Formation			Takigawa Formation	13
		Hateruma Formation	Miyakojima Limestone					20
		Fuka Formation		Naha Formation	Naha Formation	Okierabujima Formation	Hyakunodai Formation	40
Early Pleistocene								70 X10000yr
Pre-Pleistocene		Shimajiri Group	Shimajiri Group	Shimajiri Group Inogama Formation	Miyagi Formation	Neori Formation	Shimajiri Group	

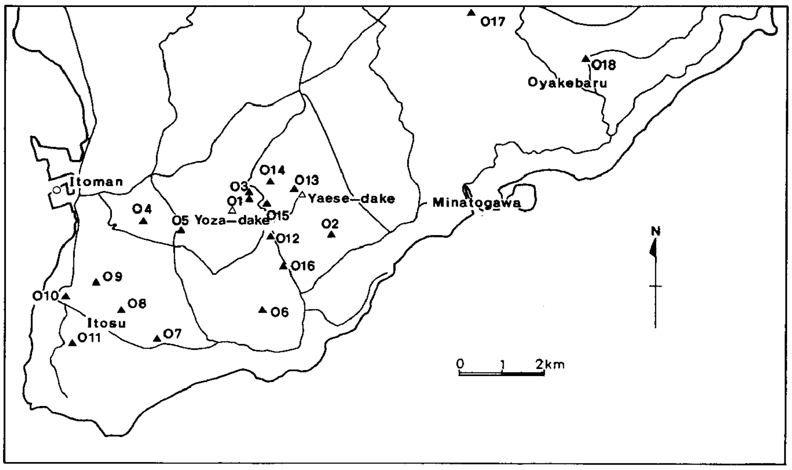


Fig. 41. Map showing localities of sketches of fossil coral communities in the southern part of Okinawa.

musica, which are hermatypic octocoral and a hydrozoan coral, were also identified (Table 13). A sclerosponge *Tabulospongia* sp. was recorded besides the corals.

Ecological studies were carried out in generic level, because the identification of fossil hermatypic corals in the specific level in the Ryukyu Group is difficult due to the poor preservation of fossils in many cases. Many arguments have been done in the generic level even in Recent corals as far as the ecological structures in vast regions are concerned.

The number of genera (N) and the value of Pielou's equitability index (J') in each island are shown in Fig. 44. Those in the southern part of Okinawa

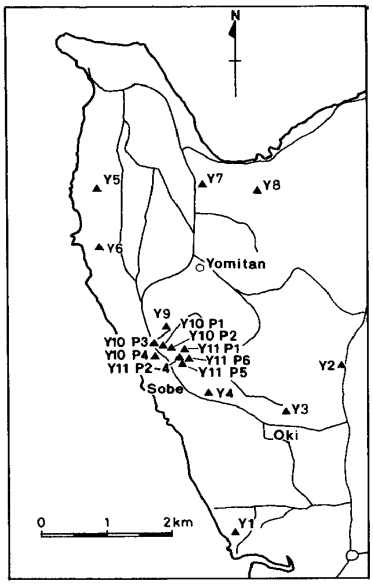


Fig. 42. Map showing localities of sketches of fossil coral communities in the Yomitan district.

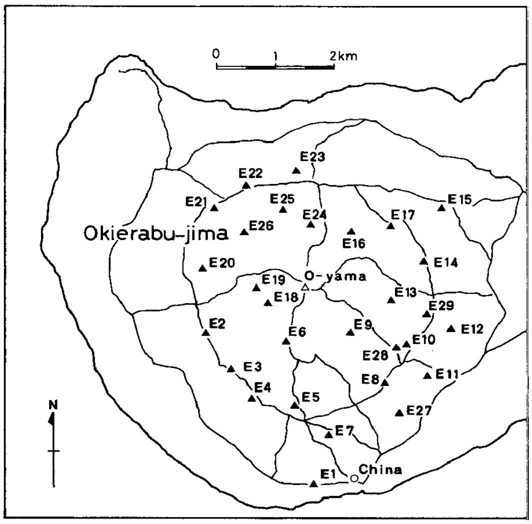


Fig. 43. Map showing localities of sketches of fossil coral communities in Okierabu-jima.

and the Yomitan district are calculated together, because these localities are closely situated to each other. The number of genera ranges from twenty-four in Kikai-jima to thirty-eight in Miyako-jima (Fig. 44). It decreases with increasing latitude. The index J' in generic level is the lowest in Hateruma-jima and the highest in Kikai-jima, and shows a tendency to increase with latitude. The fact means that each genus occupies comparatively equal volume in higher latitudes, while a few genera monopolize space in lower latitudes in the Ryukyu Islands.

b. Community

Five fossil coral communities are recognized in the Ryukyu Group based on the generic composition and sedimentological features of the limestones in which the communities are distinguished (Table 14). They are here named Communities A, B, C, D and E. Community A is characterized by the predominance of branching *Acropora* spp. and huge spherical *Porites* spp. Laminar colonies are scarcely observed. Sediment binding structure is indistinguishable in the limestone which bears the community. Community A was recorded in all the areas except for Kikai-jima. A sketch of typical example of Community A is shown in Fig. 45. Community B has a

Table 14. List of Pleistocene coral communities, their characters and comparable Recent communities.

Communities	Characteristic Taxonomic Group	Other Characters	Comparable Recent Communities
Community A	*Acropora* spp. (Branching) *Porites* spp.	Sediment Binding Structure Indistinguishable	*Porites cylindrica* Com. *Porites nigrescens* Com. *Heliopora coelurea* Com.
Community B	*Acropora* spp. (Tabular)		*Acropora hyacinthus* Com.
Community C	*Acropora* spp. (Tabular) *Porites* spp. *Favia* spp. *Platygyra* spp.		*Favia stelligera* Com.
Community D	Pectiniidae *Favia* spp. *Platygyra* spp.	Sediment Binding Structure Conspicuous	*Oxypora lacera* Com.
Community E	*Leptoseris* spp. *Pachyseris* spp.	Associated with *Cycloclypeus carpenteri*, *Operculina venosa* and Rhodolith	*Leptoseris scabra* Com.

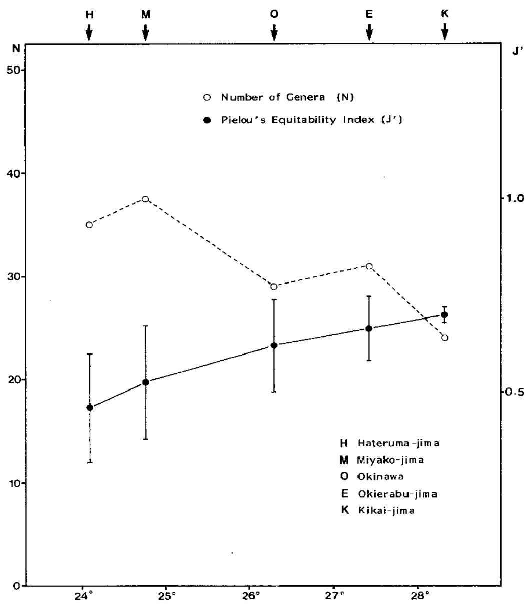


Fig. 44. Number of coral genera (N) and Pielou's equitability index (J') of each area plotted against latitude. Bars indicate the standard error ($\pm 1\sigma$).

feature that most corals are tabular *Acropora* spp. It is accompanied by hemispherical Faviinae corals, and occurs in Hateruma-jima and Miyako-jima. A sketch of Community B is shown in Fig. 46. Community C consists of tabular *Acropora* spp. and hemispherical corals such as *Favia* spp., *Porites* spp. and *Platygyra* spp. The community was recognized in almost the all areas here investigated. A typical example of the Community C is shown in Fig. 47. Community D is characterized by the presence of laminar colonies which belong to the Pectiniidae or Faviinae and by the absence of *Leptoseris* spp. The limestone bearing the community is accompanied by calcareous algae, and indicates the sediment binding structure (Fig. 48). Community D is observed in all the areas. Community E is characterized by the presence of *Leptoseris* spp. It is accompanied by *Pachyseris* spp., *Favia* spp. and Pectiniidae corals. The ratio of corals to the total rock volume is very low. The limestone which holds the community often contains rhodoliths and larger foraminifers such as *Cycloclypeus* and *Operculina*. The community is recorded in the southern part of Okinawa, Yomitan district, Okierabu-jima and Kikai-jima. A typical example of Community E is shown in Fig. 49.

c. Ratio of Corals to Total Rock Volume

Ratio of corals for each community was computed in every area (Fig. 50). The values of the mean ratio of each community range from 3 to 39%. Generally speaking, the mean ratios of each community decrease with increasing latitude. Calcareous algae instead of corals increase in high latitudes in the Ryukyu Islands. The mean ratio of Community E is less than that of the other communities.

d. Growth Rate of *Porites* spp.

In the Recent coral reefs, *Porites australiensis*, *P. lobata* and *P. lutea* have similar growth rates (Figs. 19, 20 and 21). The growth rates of fossil *Porites* spp. which probably belong to the three species mentioned above were calculated for estimation of depth range of each community. They were measured in the Communities A, D and E (Fig. 51).

Porites spp. of the Community A has the highest growth rate (8.5 mm/yr) and of the Community E has the lowest one (2.7 mm/yr) in each area. The growth rate of *Porites* spp. in each community is constant, having no relation to the latitude of the areas (Fig. 51).

4. Discussion

Diversity

In the present study, diversity of fossil corals is here discussed in comparison with that of Recent ones. The number of coral genera in the Ryukyu Group (52) is almost equal to that of the Recent corals (51). Forty genera are common both to the Recent and fossil corals. The genera found in fossil communities

Pd: *Pocillopora damicornis*
Ab: *Acropora* spp. (Branching)
At: *Acropora* spp. (Tabular)
Pv ve: *Pavona venosa*
Pa sp: *Pachyseris speciosa*
Po: *Porites* spp.
Fa: *Favia* spp.
Go as: *Goniastrea aspera*
Cs: *Cyphastrea* spp.
Tp: *Tubipora musica*
Mo: *Montipora* sp.

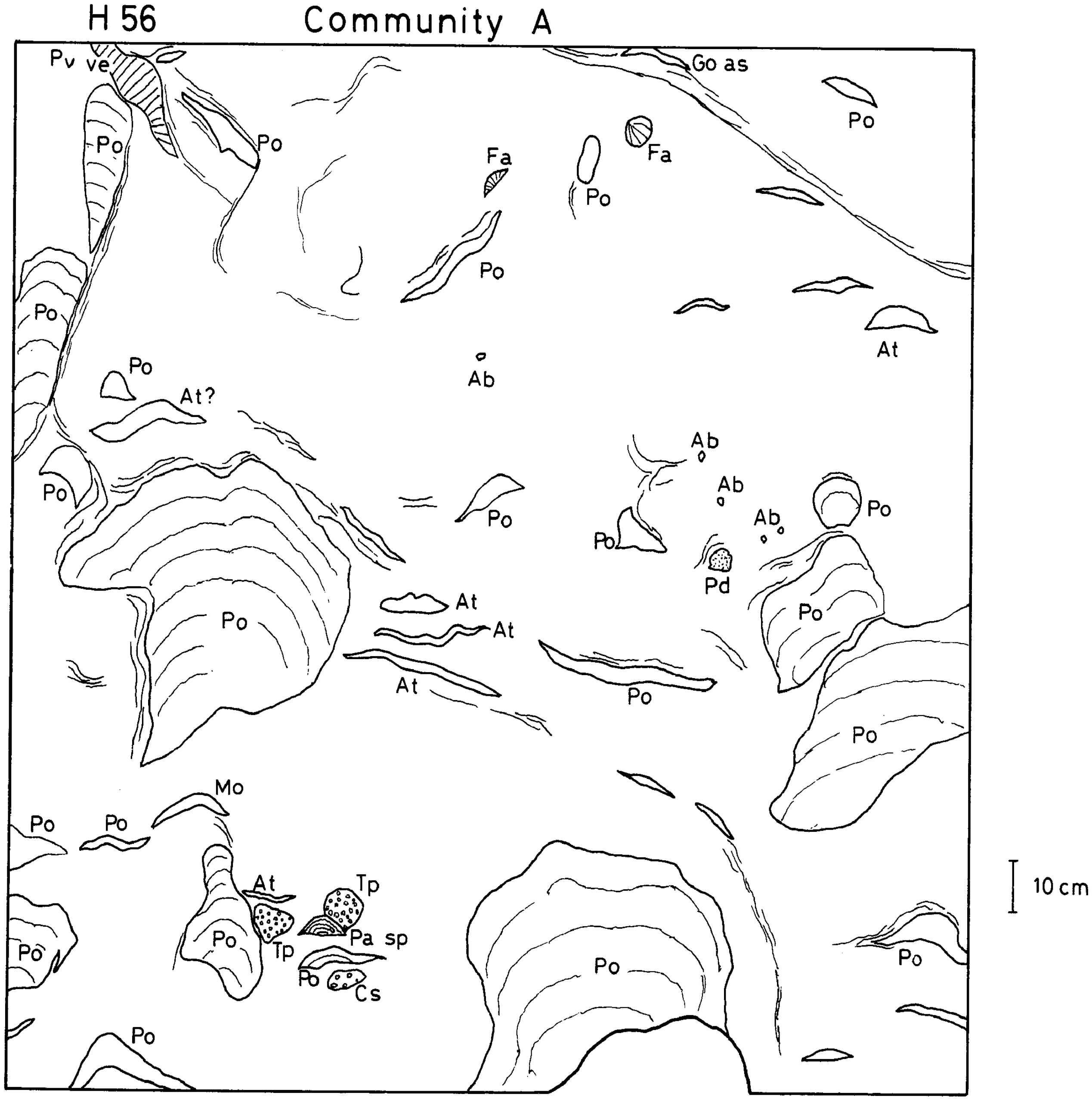
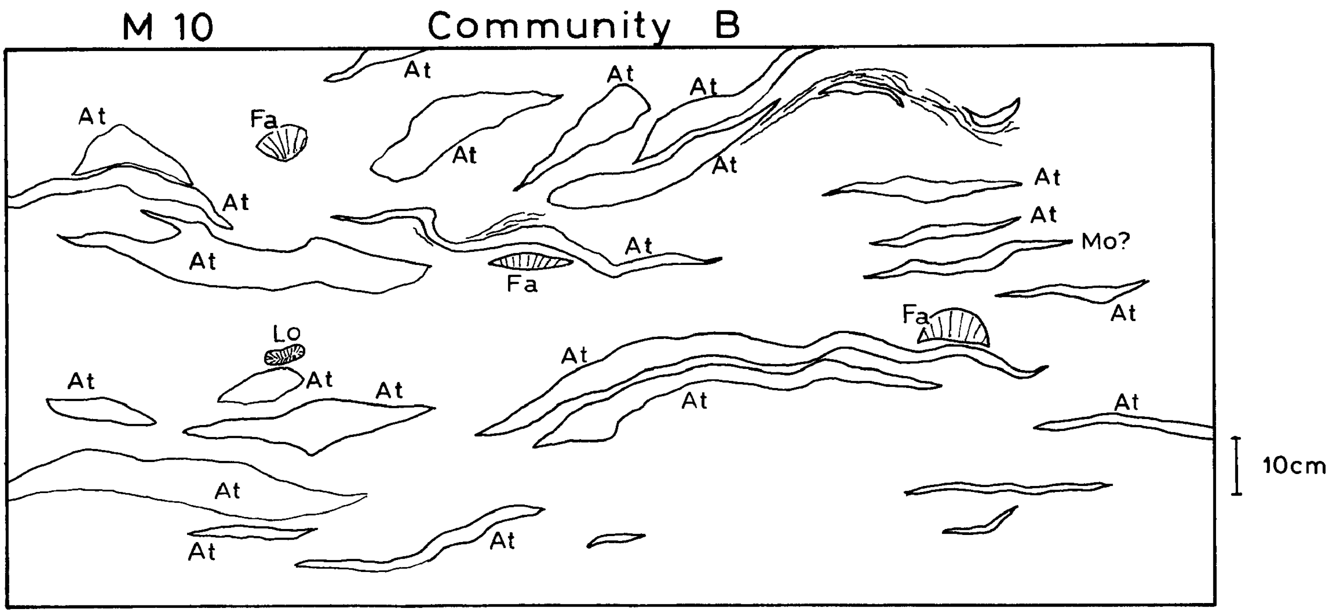


Fig. 45. Sketch of typical example of Community A in H56 (Hateruma-jima).



At: *Acropora* spp. (Tabular) Mo: *Montipora* sp.
Fa: *Favia* spp. Lo: *Lobophyllia* sp.

Fig. 46. Sketch of typical example of Community B in M10 (Miyako-jima).

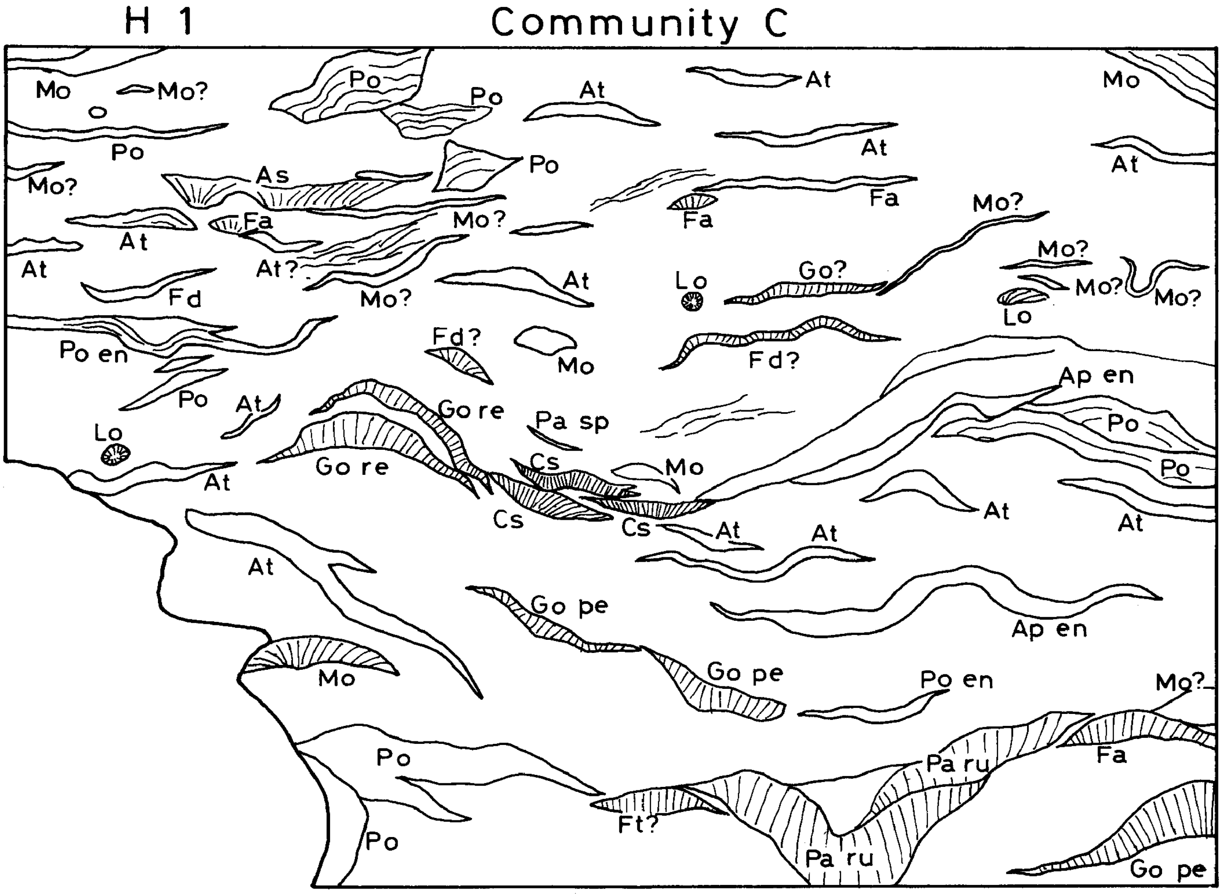
and not observed in Recent ones are mainly those living in deeper water, such as *Gardineroseris*, *Coscinaraea*, *Cycloseris* and *Trachyphyllia*. *Pavona maldivensis*, *Leptoseris yabei*, *Gardineroseris planulata*, *Favia maxima*, *Favites rotundata*, *F. russelli* and *Echinopora mammiformis* were recorded first in the Ryukyu Islands. However, less numbers of species (70) was recorded in fossil coral communities than that in Recent communities (144), because of the difficulty of identification of fossil corals in specific level.

The number of genera decreases from 38 to 24 from south to north within a distance of 4° in latitude (Fig. 44). The number of genera in each area is less than that of the whole Ryukyu Islands, because the studied areas were limited. If the decreasing rate of genera is extrapolated, the number of genera decreases about 20 towards the north within the Ryukyu Islands. This decreasing ratio is higher than that expected from the previous studies (Wells, 1954; Rosen, 1971).

The decrease of number of genera towards the north owes to the difference of water temperature rather than that of light intensity, since the solar radiation is almost the same within the Ryukyu Islands, while the water temperature steadily decreases with increasing latitude.

The ratio of the area occupied by genera such as *Porites* and *Galaxea* to the total sketched area decreases with latitude, while that of *Favia* and *Cyphastrea* increases with latitude (Table 13). The ratio of *Acropora*, the most abundant genus in the coral fauna of the Ryukyu Group seems to be constant through the Ryukyu Islands.

The increase of the equitability index (J') with latitude is considered to be due to the decrease of dominant genera such as *Porites* and *Galaxea*. The index (J') is generally lower than that of Recent corals in specific level, because many species belong to the limited genera such as *Acropora* and *Montipora* (Figs. 44, 6, 7 and 8).



At: *Acropora* spp. (Tabular) Ap en: *Acropora palifera* Mo: *Montipora* spp.
Pa ru: *Pachyseris rugosa* Po en: *Porites* spp. (Encrusting) Po: *Porites* spp.
Fa: *Favia* spp. Go pe: *Goniastrea pectinata* Go re: *Goniastrea retiformis*
Ft: *Favites* sp. Fd: Faviinae Lo: *Lobophyllia* sp. As: *Astreopora* sp.

Fig. 47. Sketch of typical example of Community C in H1 (Hateruma-jima).

Ratio of Fossil Corals to Total Rock Volume

The mean ratio of fossil corals to total rock volume ranges from 3 to 39% and is generally lower than the coverage rate of Recent corals (Figs. 9, 10 and 11). The difference between the ratio of fossil corals and the coverage rate of Recent ones is thought to be due to the difference of measuring methods ; the ratio of fossil corals indicates the real ratio of corals to the total space, while the coverage rate of Recent corals is the ratio of corals projected on a horizontal plane to the total area.

The mean ratio of corals decreases with latitude (Fig. 50), while the growth rates of the fossil and Recent *Porites* spp. are constant in the Ryukyu Islands (Figs. 51, 19, 20 and 21). If the growth rates of corals in the Ryukyu Group are presumed to be constant, the decrease of coral ratio with latitude is considered to be due to the decrease of number of colonies per unit area with latitude.

Depositional Environment of the Ryukyu Group

The Pleistocene Ryukyu Group contains sediments of coral reefs. But, only a few studies on the depositional environment of the Ryukyu Group have been carried out, although there are many stratigraphic and sedimentological studies (Takayasu, 1978 ; Kameyama and Shuto, 1980 ; Nakamori, 1982 ;

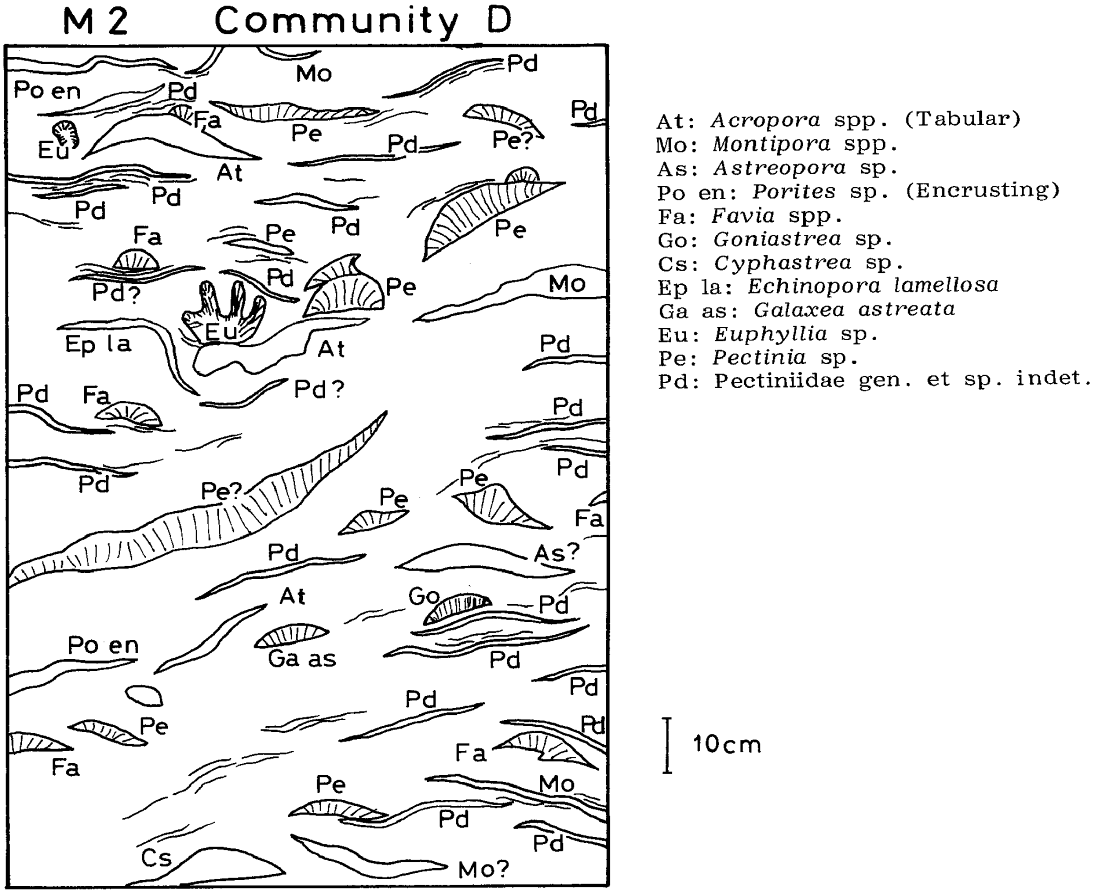


Fig. 48. Sketch of typical example of Community D in M2 (Miyako-jima).

Noda, 1984b). The ecological data from the Recent hermatypic corals and other organisms seem to be helpful when the depositional environments of the Ryukyu Group are discussed.

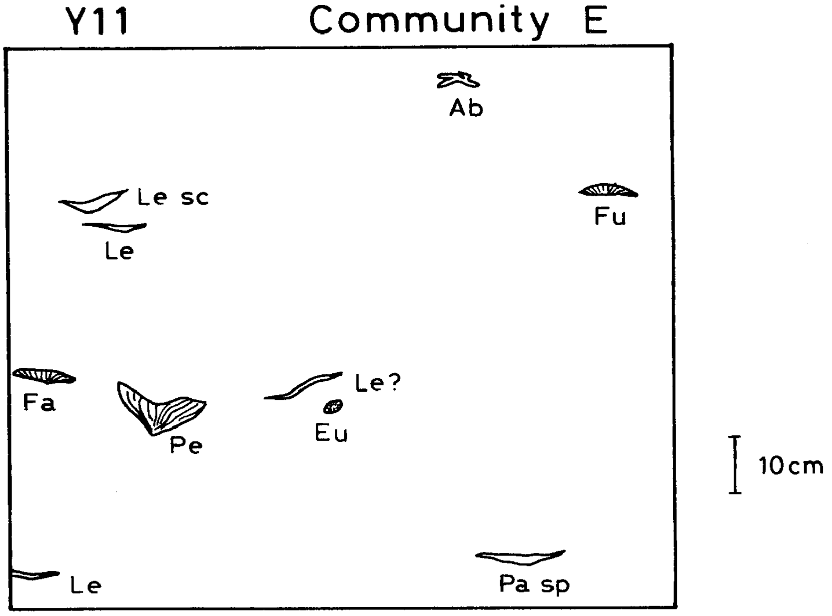
Rocks which constitute the Ryukyu Group are divided into six groups based on the lithofacies and biofacies of limestone (Minoura, 1979; Nakamori, 1982). They are coral, rhodolith, detrital, *Cycloclypeus-Operculina* limestones, calcareous sandstone and conglomerate. The depositional environment of each rock type is considered as follows.

1) Coral Limestone

Five fossil coral communities were recognized in the coral limestone of the Ryukyu Group. A paleoenvironment in which each community lived is estimated based on the correlation to the Recent communities and the growth rate of *Porites* spp.

Community A: Community A can be correlated to the Recent *Porites cylindrica*, *P. nigrescens* and *Heliopora coerulea* communities, because it contains numerous branching *Acropora* spp., *Montipora* spp. and hemispherical *Porites* spp. (Table 14). The growth rate of *Porites* spp. in the Community A is about 8 mm/yr and indicates that the depth in which the community existed is shallower than several meters (Figs. 51, 19, 20 and 21). Consequently, Community A is distributed from the moat to the reef crest of fringing reef or in a protected shallow water of patch reefs.

Community B: Community B is characterized by the dominance of tabular *Acropora* app. and correlated to the Recent *Acropora hyacinthus* Community. So, the community is considered to have



Ab: *Acropora* sp. (Branching)
Fu: *Fungia* sp.
Le sc: *Leptoseris scabra*
Pa sp: *Pachyseris speciosa*
Fa: *Favia* sp.
Eu: *Euphyllia* sp.
Pe: *Pectinia* sp.
Le: *Leptoseris* sp.

Fig. 49. Sketch of typical example of Community E in Y11 (Yomitan district).

lived in the reef edge which stands at almost sea level.

Community C: Community C is characterized by the presence of tabular *Acropora* spp., hemispherical *Porites* spp., *Favia* spp. and *Platygyra* spp., and the absence of the pectiniid genera such as *Echinophyllia*, *Oxypora* and *Mycedium* (Table 14). The generic composition and morphological features indicate that Community C can be correlated to the Recent *Favia stelligera* Community. The growth rate of *Porites* spp. in Community C (5 mm/yr) is the same as that of Recent *Porites* spp. at 10 m depth, and supports the correlation (Figs. 51, 19, 20 and 21). Thus, the community is thought to have inhabited water depths of 0 m to 15 m on the reef slope.

Community D: Community D is equivalent to the Recent *Oxypora lacera* Community, because the community contains the pectiniid genera such as

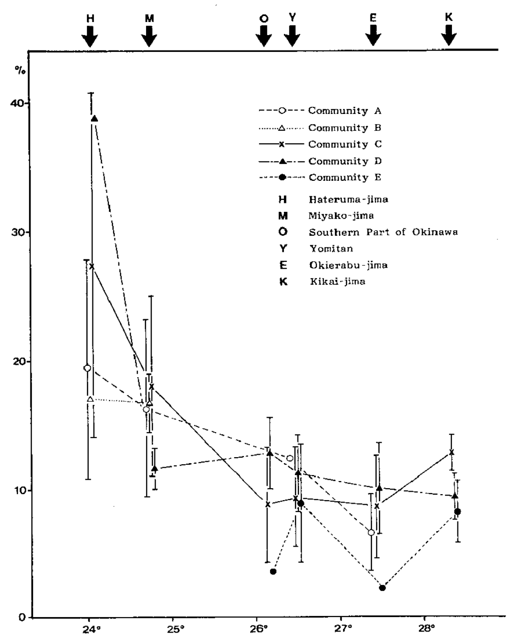


Fig. 50. Mean ratio of corals of each community in six areas to the total rock volume. Bars indicate standard error ($\pm 1\sigma$).

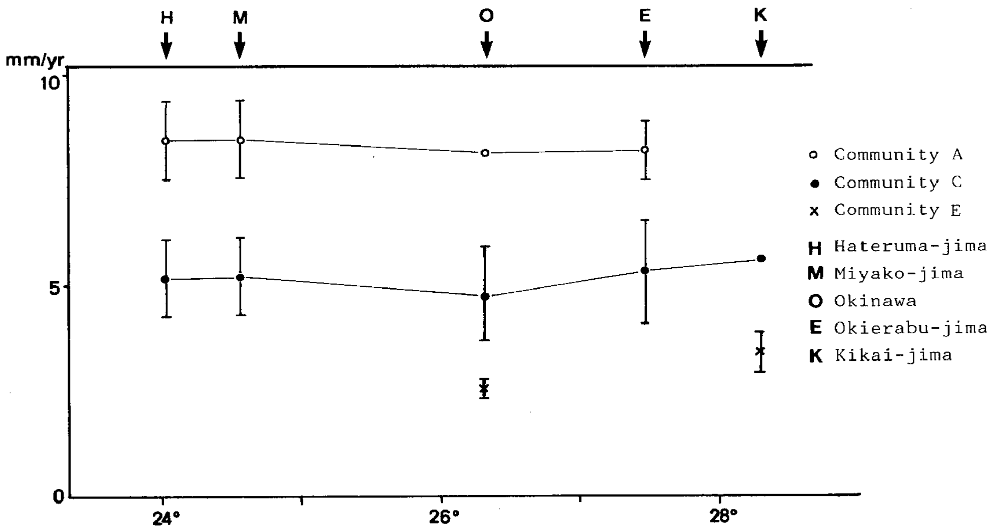


Fig. 51. Growth rates of *Porites* spp. in Communities A, C and E in five islands.

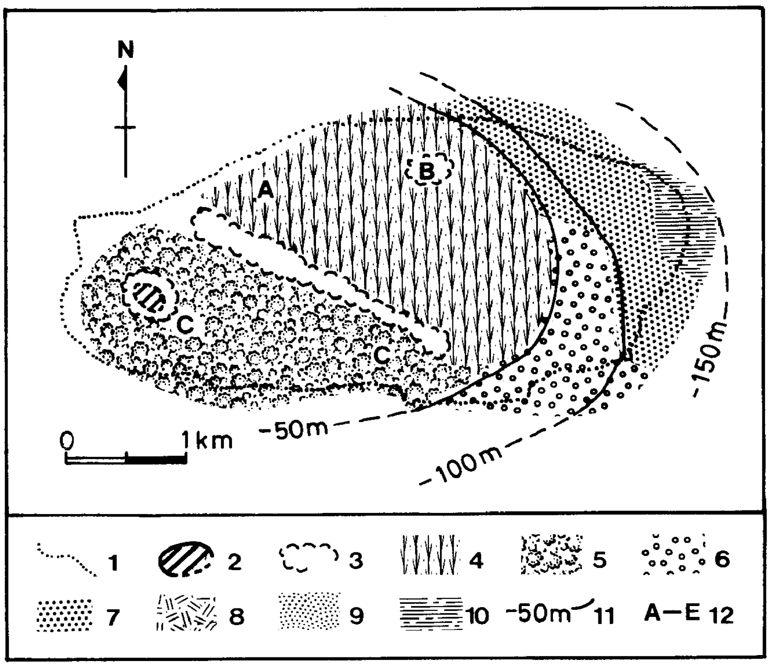


Fig. 52. Paleogeographic map of Hateruma-jima when the Hateruma Formation was deposited.
1 : Outline of present island ; 2 : Land ; 3 : Reef facies ; 4 : Backreef facies ; 5 : Forereef facies ; 6 : Rhodolith facies ; 7 : Detrital facies ; 8 : Gravel facies ; 9 : Calcareous sand facies ; 10 : *Cycloclypeus-Operculina* facies ; 11 : Depth contour line ; 12 : Communities A-E.

Echinophyllia, *Oxypora* and *Mycedium* (Table 14). The fact that laminar colonies predominate the Community D supports the correlation (Fig. 15). Consequently, the community is considered to have lived from 10 to 30 m in depth on the reef slope.

Community E : Community E has similar genera, such as *Leptoseris* and *Pachyseris*, to those of the Recent *Leptoseris scabra* Community. So, it is correlated to the *L. scabra* Community which occurs deeper than 30 m on the reef slope (Table 5). Yamazato (1971) mentioned that the deeper layer zone in which an equivalent community to the *L. scabra* Community inhabits ranges from 50 to 100 m in depth. Consequently, the depth range of Community E is thought to be from 30 to 100 m. The fact that the community is frequently accompanied by rhodoliths and *Cycloclypeus carpenteri* (larger foraminifer) supports the depth range of the community.

Depositional environments of the coral limestone which bears those communities are inferred by the paleoenvironments of each community.

2) Rhodolith Limestone

Minoura (1979) and Minoura and Nakamori (1982) discussed depositional environment of rhodoliths based on sedimentological evidence. They concluded that the rhodoliths grow during transportation through channels shallower than 30 m, and that they concentrate on the deeper flat plain. Noda (1984b) estimated the depth range of the rhodoliths from 50 to 150 meters based on stratigraphic information.

Recent rhodoliths were reported from both the Indo-Pacific and Atlantic regions (Bosellini and Ginsburg, 1971 ; Adey and MacIntyre, 1973 ; Nohara *et al.*, 1979 ; Bouchon, 1981 ; Iryu 1984, 1985 ; Iryu and Hayasaka, 1985). Their distribution ranges from 0 to 200 m in depth and most of them are restricted to a depth ranging from 50 m to 120 m. Around the Ryukyu Islands, Recent rhodoliths were obtained on the shelves (86–115 m depth) off Tarama-jima in the southern part of the Ryukyu Islands (Iryu, 1984, 1985).

Consequently, the rhodolith limestone is thought to have deposited on the shelf at depths between 50 m and 120 m around the coral reefs.

3) Detrital Limestone

Detrital limestone is divided into two types. One of them consists of coarse to medium size grains, most of which are composed of worn tests of foraminifers, algae, corals and molluscs. This type does not contain micrite and indicates grain-supported sedimentary texture. Cross beds are frequently observed. Consequently, it is thought to have been deposited under conditions of high hydrodynamic energy. The limestone of this type laterally changes into coral limestone or is intercalated with the latter. Therefore, it is considered to have been deposited in the moat or shallow inter-reef areas. The detrital limestones of the Minatogawa Formation in Ikei-jima and southern part of Okinawa belong to this type. The other type is composed of grains fine to medium in size and micritic matrix or sparry cement. It contains solitary corals, rhodoliths, brachiopods, bryozoans and molluscs in places. It occurs chiefly outside the coral or rhodolith limestone. Consequently, most parts of the detrital limestone of this type are thought to have been deposited at depths exceeding 50 m along the outer margin of the coral reefs.

4) *Cycloclypeus-Operculina* Limestone

Cushman *et al.* (1954) reported the Recent *Cycloclypeus carpenteri* from 104 to 432 m in depth in Bikini Atoll. In the Ryukyu Islands, *Cycloclypeus* was obtained from 70 to 235 m in depth and known to concentrate at depths in the range of 80 m to 130 m (Hanzawa, 1948, 1951 ; Yamazato *et al.*, 1967 ; Iryu, 1984). Therefore, *Cycloclypeus-Operculina* limestone is thought to have deposited mainly at 80–130 m depth. Since it is frequently found in the lowest horizon of a sedimentary cycle of the Ryukyu Group, the limestone is considered to have been deposited on the shelf (80 to 130 m in depth) prior to rhodolith or detrital sediment accumulation (Takayasu, 1978 ; Nakamori, 1982).

5) Calcareous Sandstone

Calcareous sandstone consists of carbonate grains, terrigenous silt and sand. It is accompanied by *Cycloclypeus*, *Operculina*, rhodolith, brachiopods and molluscs. The sandstone is frequently found just on the basement of the Ryukyu Group. Those facts mean that the sandstone have been deposited on the shelf (80 to 130 m depth) to which terrigenous silts and sands flowed down.

6) Conglomerate

Conglomerate in the Ryukyu Group consists of granule to cobble size gravels of the basement rocks, and scarcely contains carbonate sediments. The gravels are angular or subangular. Fragments of plants are observed in places. Most parts of the conglomerate occur between the basement and the limestones. Therefore, the conglomerate was deposited in the very shallow water where corals could not live due to the influx of terrigenous sediments.

Paleogeography

Paleogeography is reconstructed in the six areas based on the stratigraphy and the distributions of each lithofacies. Paleogeographical maps and the distribution of the five coral communities are shown in Figs. 52-57. The generalized paleogeographic maps and coral communities plotted on the maps are not necessarily of exactly the same age. An area from moat to outer reef flat of a fringing reef and a shallow area protected by patch reefs are here called "backreef", and a part which corresponds to the reef edge is here named "reef". "Forereef" is used for the reef slope of the Recent reefs.

1) Hateruma-jima

A paleogeographic map of the stage when the Hateruma Formation was deposited is shown in Fig. 52. Judging from the distribution of coral communities, backreef is thought to have existed in the northern and central part the island and forereef in the southwestern part of the island. Reefs have probably developed between them. Carbonate detrital sediments and rhodoliths were deposited in the northeastern and southeastern parts of the backreef, respectively. *Cycloclypeus* distributed outside the detrital facies. The water depth is thought to have been constant in the backreef. But, it seems to have increased suddenly around the backreef until it reached about 100 m in depth, judging from the distribution of the limestones.

The reef in the ancient Hateruma-jima is considered to be an aggregation of patch reefs which had the reef edges in its southern part.

2) Miyako-jima

The distributions of the communities indicate that the backreef was situated mainly along the northeastern coast of the present Miyako-jima and the forereef in most part of the island (Fig. 53). Reefs are inferred to have existed between the backreef and the forereef along the southern coast of the present Miyako-jima. Detrital sediments were distributed in the southern and northern margins of the forereef. *Cycloclypeus* and *Operculina* inhabited outward of the detrital facies. The reef complex grew on the flat base. Owing to the distribution of each limestone, the southern and northern margins of the base are considered to be very steep slopes which reached 150 m in depth. The fact that rhodoliths can not be seen in this stage seems to be due to the topography of the reef complex. It is likely that a land existed to the east of the reefs, since fossil mammals were reported from the Holocene sediments of Miyako-jima (Tokunaga and Takai, 1938; Tokunaga, 1940; Hasegawa *et al.*, 1973), although the island is now completely covered with the Ryukyu Group. The paleogeographic map in Fig. 53 is of the stage when the lower part of the Miyako-jima Limestone deposited (Nakamori, 1982).

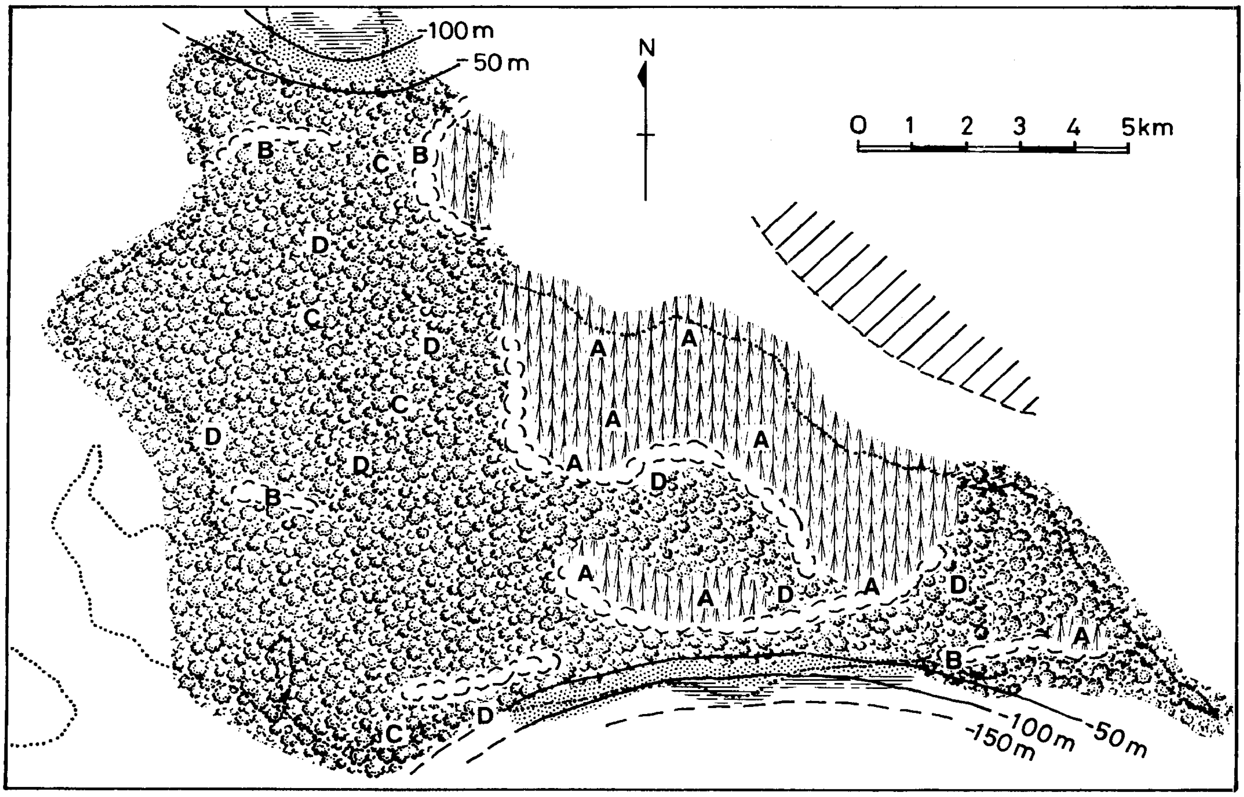


Fig. 53. Paleogeographic map of Miyako-jima when the lower part of the Miyako-jima Limestone was deposited. Legend is shown in Fig. 52.

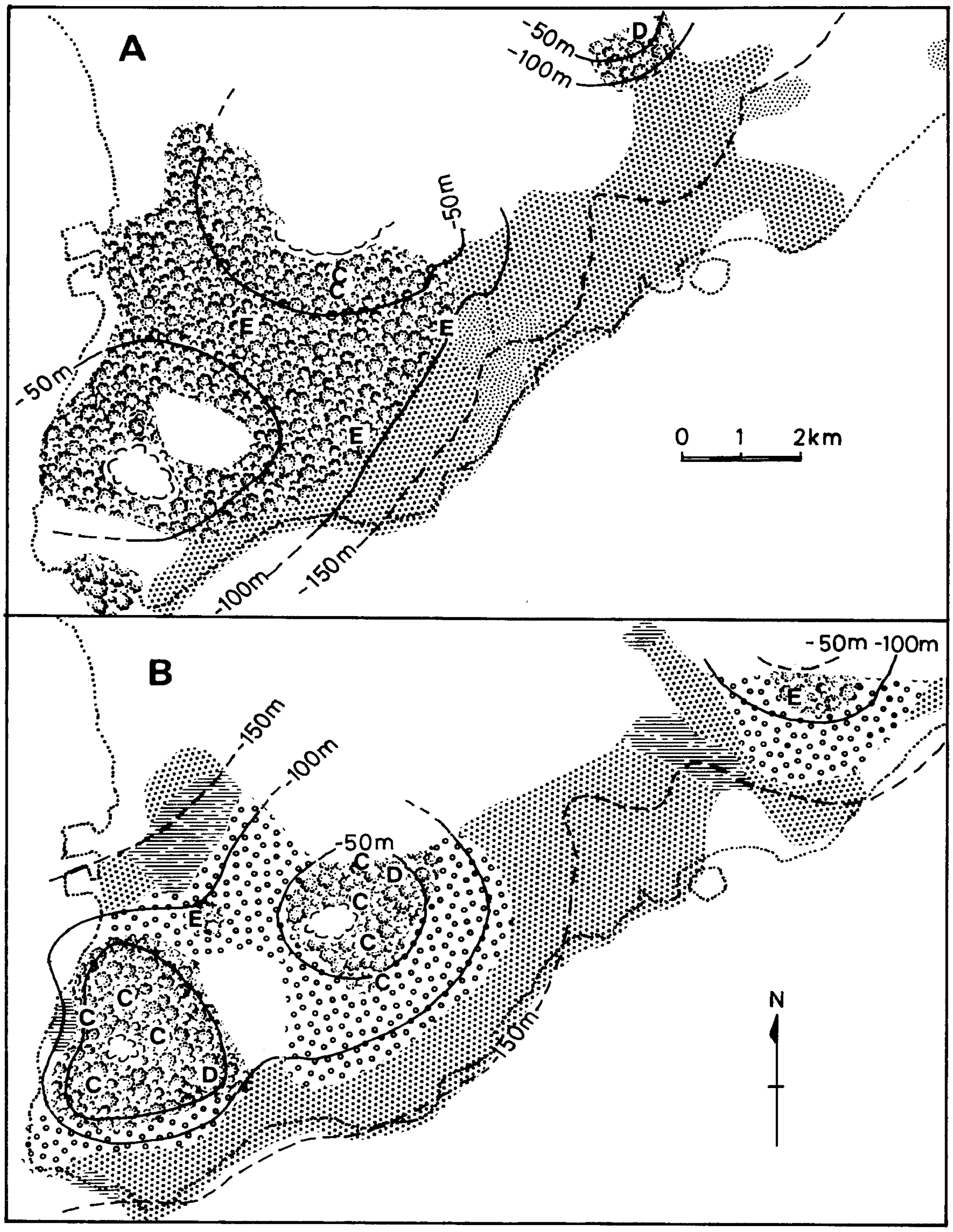
The reef complex of the ancient Miyako-jima in this stage is thought to have been formed by the patch reefs like Yaebishi which is situated to the north of the present Miyako-jima.

3) Southern Part of Okinawa

Paleogeographic maps of the southern part of Okinawa in the stages when the lower part and the upper part of the Naha Formation were deposited are shown in Figs. 54 A and B, respectively.

In the stage when the lower part was deposited, it seems that there have been three centers of reef complex in the southern part of Okinawa, judging from the distribution of the coral limestone and coral communities. The centers were situated around the present Oyakebaru, Yoza-dake, and Itosu, Itoman City (Fig. 54 A). Detrital sediments are distributed along the southern circumference of these reef complexes. Calcareous sandstone was deposited to the southeast of the Oyakebaru and Yoza-dake reef complexes. The distal part of the detrital limestone is thought to have been deposited at depths of greater than 100 m as estimated from the stratigraphic position of the detrital limestone.

The sea level is considered to have gradually rised from the early to late stages of the Naha Formation, because the coral limestone of the Naha Formation was deposited continuously and reached about 30 m in thickness (Fig. 30). In the late stage, three reef complexes were developed in the areas where the previous ones had existed (Fig. 54 B). They were reduced, and consist of small patch reefs without any backreef facies. Rhodoliths were deposited on the plain which had been constructed by the coral limestone in previous stage. Detrital sediments occurred along the southern margin of the reef complexs. *Cycloclypeus* and *Operculina* mainly



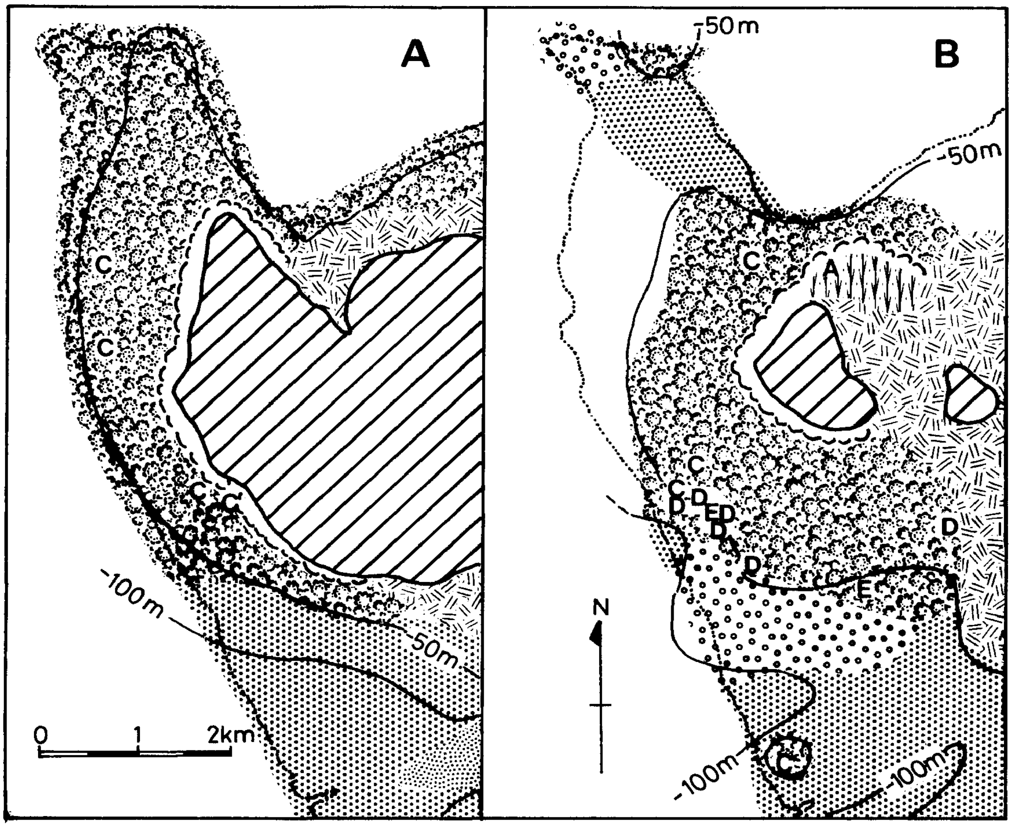
Figs. 54A, B. Paleogeographic maps of the southern part of Okinawa when the lower part (A) and the upper part (B) of the Naha Formation were deposited. Legend is shown in Fig. 52.

inhabited to the north of Itosu Reef Complex and to the southwest of Oyakebaru Reef Complex.

4) Yomitan District

Paleogeographic maps of the early and late stages of the Naha Formation in the Yomitan distric are shown in Figs. 55 A and B, respectively.

In the early stage, a land is thought to have existed in the central part of this district. Fringing reefs were formed along the west coast of the land, but the backreef facies was not developed. Forereef is distributed widely to the north and east of the land. Gravels were deposited instead of the coral lime-



Figs. 55A, B. Paleogeographic maps of the Yomitan district when the lower part (A) and the upper part (B) of the Naha Formation were deposited. Legend is shown in Fig. 52.

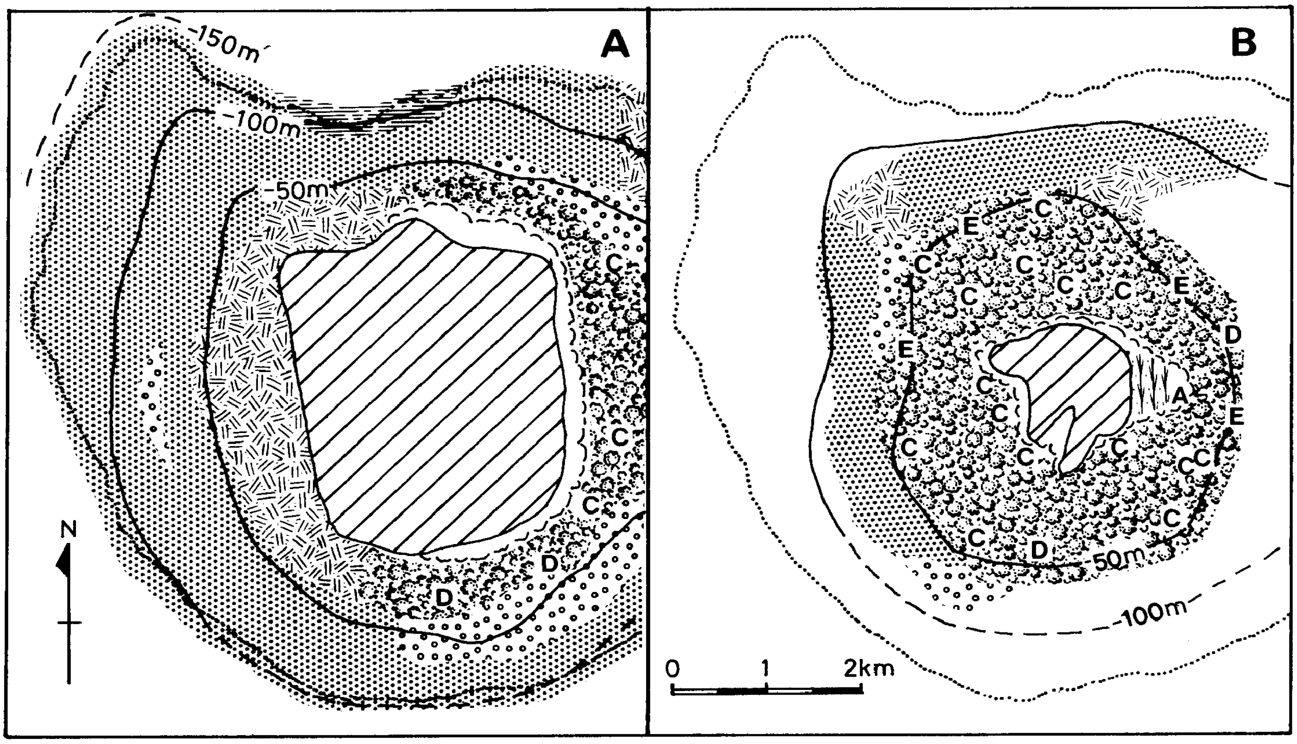
stone to the north and south of the land. Detrital facies are found to the south of the gravel and coral facies. Calcareous sandstone was deposited in the valley in the southern part of this area. The depth of the valley is considered to be about 100 m according to the starati-graphic position of the sandstone.

In the late stage, the sea level was higher than that in the early stage. The land was reduced to small islands. Reefs were developed to the west of the islands and backreef facies also existed in some parts. Small patch reefs were formed in the northern and southern parts of the area. Gravels continued to accumulate in the eastern part of the area. Rhodoliths were deposited to the south of the main coral reef. The detrital facies was distributed to the south of the rhodolith facies and to the north of the main reef.

5) Okierabu-jima

Paleogeographic maps of the early and late stages of the Okierabu-jima Formation are shown in Figs. 56 A and B, respectively.

In the early stage, an island was situated in the area whose highest part was at the present O-yama. Fringing reefs developed along the east side of the island, but the backreef did not spread here. Forereef was distributed off the western half of the island, while gravels were deposited off the eastern half of the island. Detrital sediments surrounded the forereef and gravel facies. They are thought to have reached more than 150 m in depth, judging from their stratigraphic position. Rhodoliths were deposited in some areas where were about 50 m in depth. *Cycloclypeus* and *Operculina* inhabited to the north of the detrital facies and its depth is thought to



Figs. 56A, B. Paleogeographic maps of Okierabu-jima when the lower part (A) and the upper part (B) of the Okierabu-jima Formation were deposited. Legend is shown in Fig. 52.

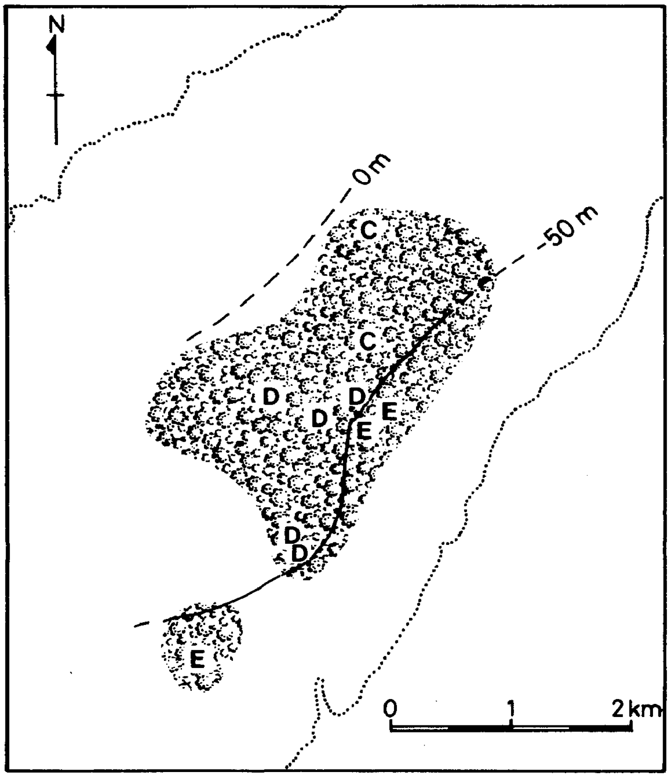


Fig. 57. Paleogeographic map of Kikai-jima when the Takigawa Formation was deposited. Legend is shown in Fig. 52.

have been more than 100 m.

In the late stage of the Okierabu-jima Formation, the sea level rose and the island was narrowed. Reefs enclosed the island and backreef developed in places. Forereef surrounded outside the reefs. Detrital sediments occurred to the north and east of the forereef, and its distal part reached more than 100 m in depth. Rhodoliths were deposited sporadically in the detrital facies.

6) Kikai-jima

A paleogeographic map in the stage when the Takigawa Formation was deposited is shown in Fig. 57. Forereef was distributed in the present Hyakunodai. The topography of the forereef is considered to decline to southwest judging from the distribution of coral communities. A depth contour of 50 m is supposed to have lain along the southeast margin of the present Hyakunodai.

Two types of the reef complex are recognized in the Ryukyu Group. One of them is a fringing reef and the other is the aggregation of patch reefs. The former is seen in the areas where the basement is composed of hard sandstone and slate, for example, Yomitan district and Okierabu-jima (Figs. 55 and 56). The latter occurs in the areas whose basement is the Shimajiri Group composed of weakly consolidated sand and silt, such as Hateruma-jima, Miyako-jima and southern part of Okinawa (Figs. 52, 53 and 54). A soft basement such as the Shimajiri Group is considered to have had a tendency to form flatter topography than a hard one, because of the weakness to erosion. The coral reef complex of the Ryukyu Group in Kikai-jima is thought to be a type of aggregation of patch reefs.

CONCLUSION

(1) Recent coral reefs in Ishigaki-jima and Sesoko-jima consist of six topographic areas. They are moat, inner reef flat, reef crest, outer reef flat, reef edge and reef slope from shore to offshore.

(2) Fifty-one coral genera and 144 coral species are recorded in the Recent coral reefs. The number of species, Shannon-Weaver's diversity index (H'), Pielou's equitability index (J') and coverage have two modes within a reef and their lowest peak in the outer reef flat.

(3) Diversity (H') has the highest values when coverage is about 50%. Equitability (J') and coverage rate indicate a weak negative correlation in each topographic area. The relation between them can be explained by the intermediate disturbance hypothesis proposed by Connell (1978).

(4) Ten communities are recognized in the Recent coral reefs in Ishigaki-jima and Sesoko-jima. They can be correlated to those previously reported in the Ryukyu Islands and some of Indo-Pacific reefs. Each community has a specific distribution range in a reef. But some communities live together in a certain area of a reef. On the other hand, different communities are observed in an equivalent environment of different reefs in some cases.

(5) The growth form of Recent hermatypic corals is divided into 11 types. The composition of growth form in a certain area of a reef is constant in the Ryukyu Islands and many reefs in other regions.

(6) *Porites* spp. changes its growth form with depth. A model to interpret the change of the form is made based on the growth rate of a corallum and the increasing rate of the surface area of a corallum.

(7) The stratigraphy and chronology of the Ryukyu Group in Hateruma-jima, Miyako-jima, Okinawa, Okierabu-jima

and Kikai-jima are clarified. The formations in these areas are correlated with each other.

(8) Fifty-two genera and 70 species of fossil corals are identified in the Ryukyu Group. The number of genera decreases with latitude in the Ryukyu Islands, while equitability (J') increases with latitude.

(9) Five communities are recognized in fossil corals of the Ryukyu Group. They can be correlated to the Recent communities in the Ryukyu Islands. Paleoenvironments of the fossil communities are reconstructed based on the correlation.

(10) The ratio of fossil corals to the total rock volume decreases with latitude in the Ryukyu Islands. The ratio of Community E is lower than that of the other communities of the Ryukyu Group.

(11) The growth rate of the coralla of fossil *Porites* spp. in Communities A, C and E is constant within the Ryukyu Islands. *Porites* spp. in the Community A has the highest rate and that in the Community E has the lowest among the three communities.

(12) Paleogeographic maps of the stages when the Takanasaki, Naha, Okierabujima and Takigawa Formations and Miyakojima Limestone were deposited are reconstructed based on the depositional environments of the fossil coral communities and the limestones.

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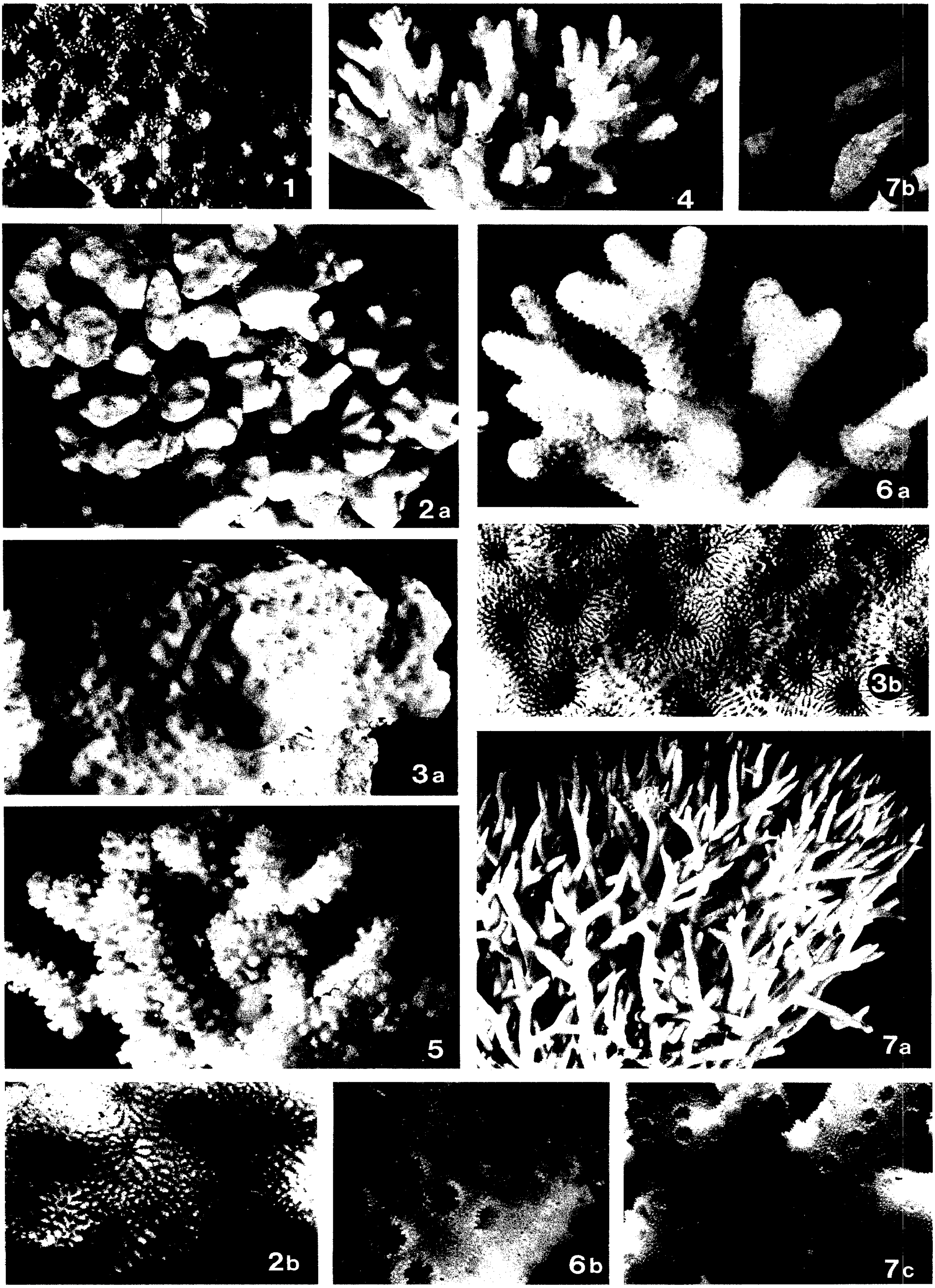
Plate 1

Fig. 1. *Stylocoeniella armata* (Ehrenberg, 1834)
St. 2, Tr. 6, Yonehara, Ishigaki-jima. ×5.
Figs. 2a, b. *Psammocora contigua* (Esper, 1797)
Kabira Cove, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.
Figs. 3a, b. *Psammocora profundacella* Gardiner, 1898
St. 1, Tr. 6, Kabira, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.
Fig. 4. *Pocillopora damicornis* (Linnaeus, 1758)
St. 1, Tr. 6, Kabira, Ishigaki-jima. ×1.
Fig. 5. *Pocillopora verrucosa* (Ellis & Solander, 1786)
St. 1, Tr. 30, Kabira, Ishigaki-jima. ×0.67.
Figs. 6a, b. *Stylophora pistillata* Esper, 1797
St. 1, Tr. 18, Kabira, Ishigaki-jima.
Fig. 6a, ×1, Fig. 6b, ×5.
Figs. 7a-c. *Seriatopora hystrix* Dana, 1846
St. 1, Tr. 31, Kabira, Ishigaki-jima.
Fig. 7a, ×0.67, Figs. 7b, c, ×5.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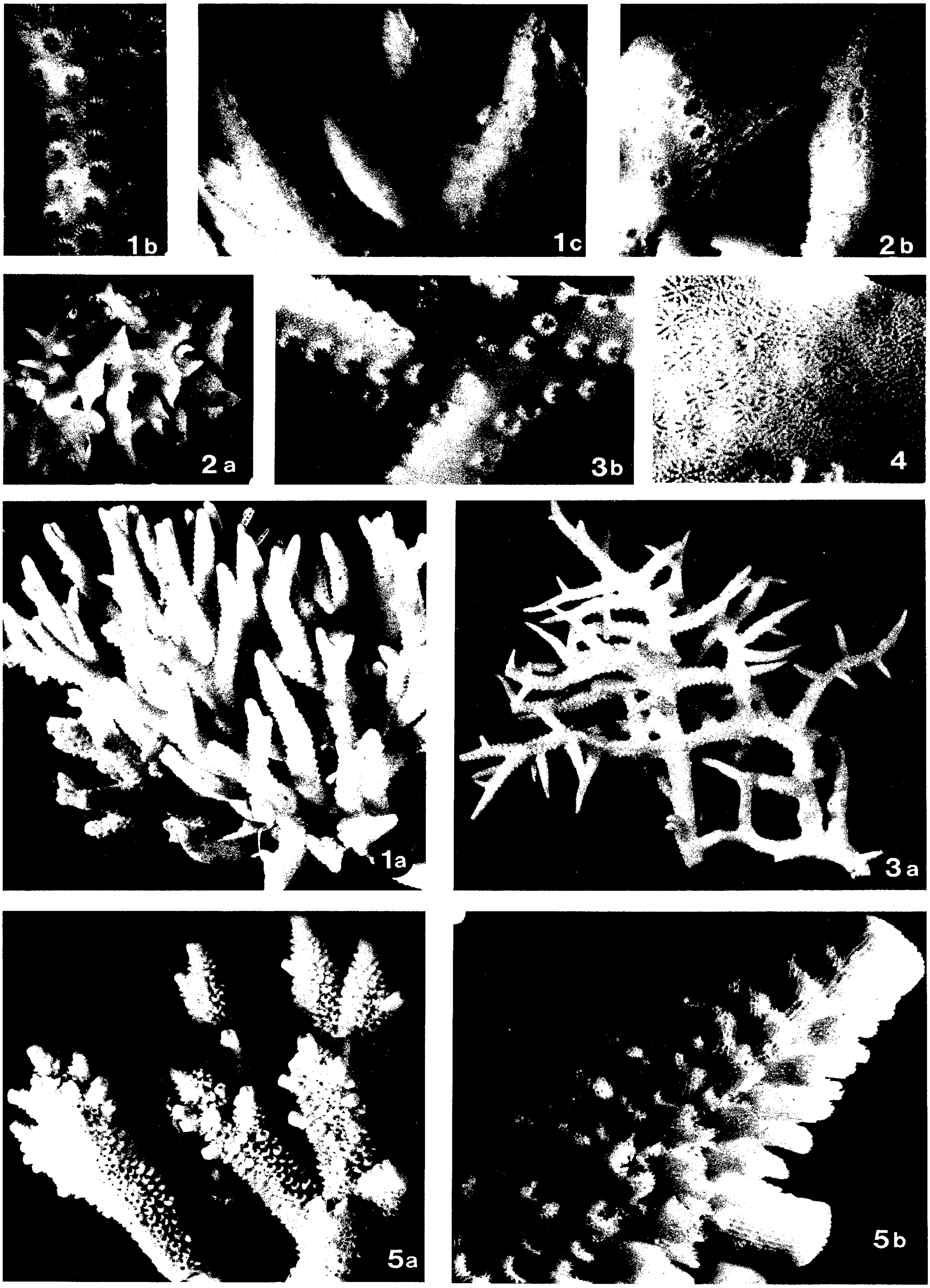
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Plate 2

Figs. 1a-c. *Seriatopora caliendrum* Ehrenberg, 1834
St. 1, Tr. 21, Kabira, Ishigaki-jima.
Fig. 1a, $\times 1$, Figs. 1b, c, $\times 5$.
Figs. 2a, b. *Seriatopora* sp. A
St. 1, Tr. 30, Kabira,Ishigaki-jima.
Fig. 2a, $\times 1$, Fig. 2b, $\times 5$.
Figs. 3a, b. *Seriatopora* sp. B.
St. 1, Tr. 31, Kabira, Ishigaki-jima.
Fig. 3a, $\times 1$, Fig. 3b, $\times 5$.
Fig. 4. *Palaustrea ramosa* Yabe & Sugiyama, 1941
Sesoko-jima, Okinawa. $\times 5$.
Figs. 5a, b. *Acropora aspera* (Dana, 1846)
St. 3, Tr. 18, Shiraho, Ishigaki-jima.
Fig. 5a, $\times 1$, Fig. 5b, $\times 5$.

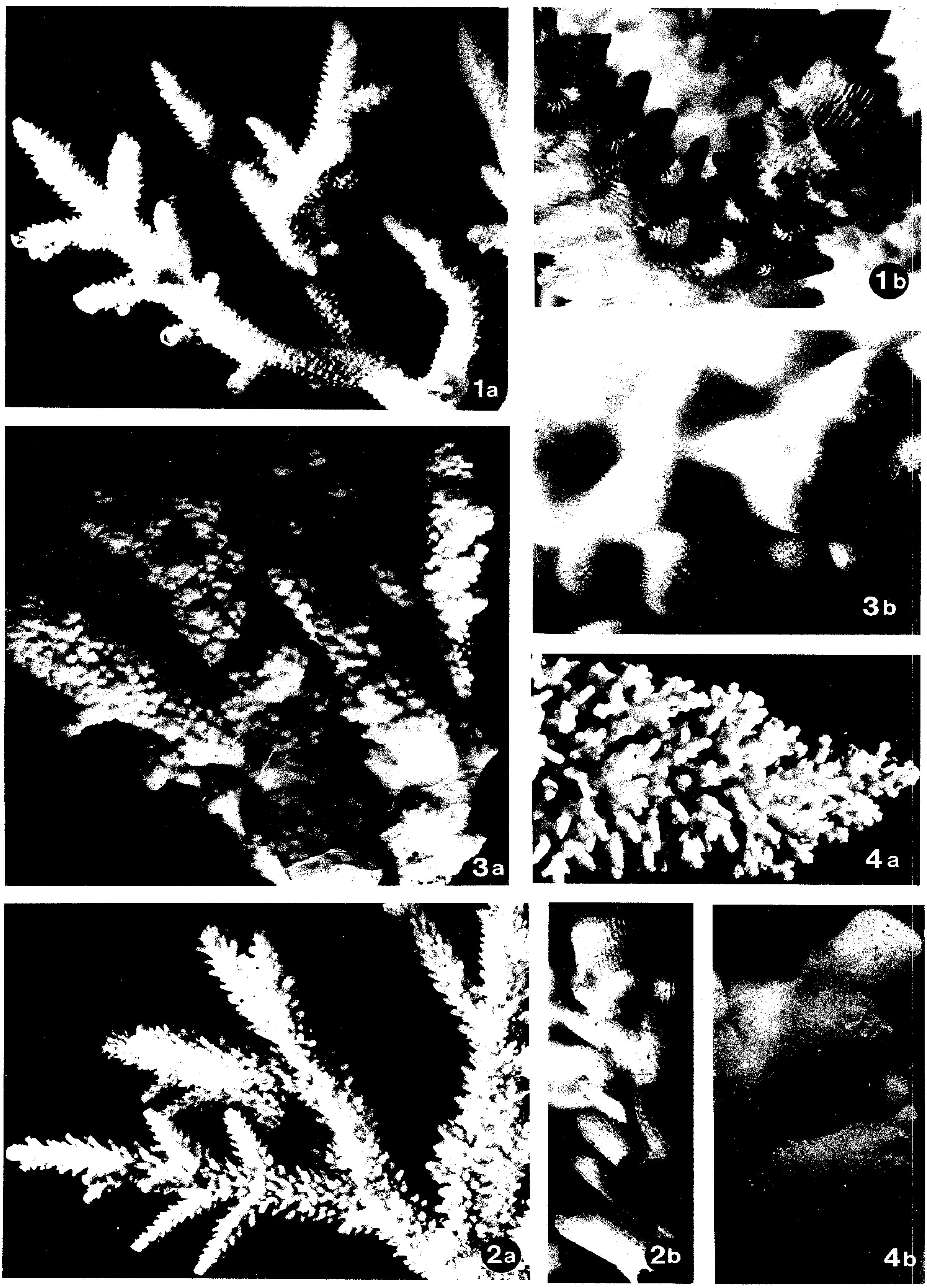
Plate 3

Figs. 1a, b. *Acropora aspera* var. *hebes* (Dana, 1846)
St. 3, Tr. 10, Shiraho, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a, b. *Acropora acuminata* (Verrill, 1864)
St. 1, Tr. 30, Kabira, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×5.

Figs. 3a, b. *Acropora brueggemanni* (Brook, 1893)
St. 3, Tr. 12, Shiraho, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×5.

Figs. 4a, b. *Acropora carduus* (Dana, 1846)
St. 1, Tr. 15, Kabira, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.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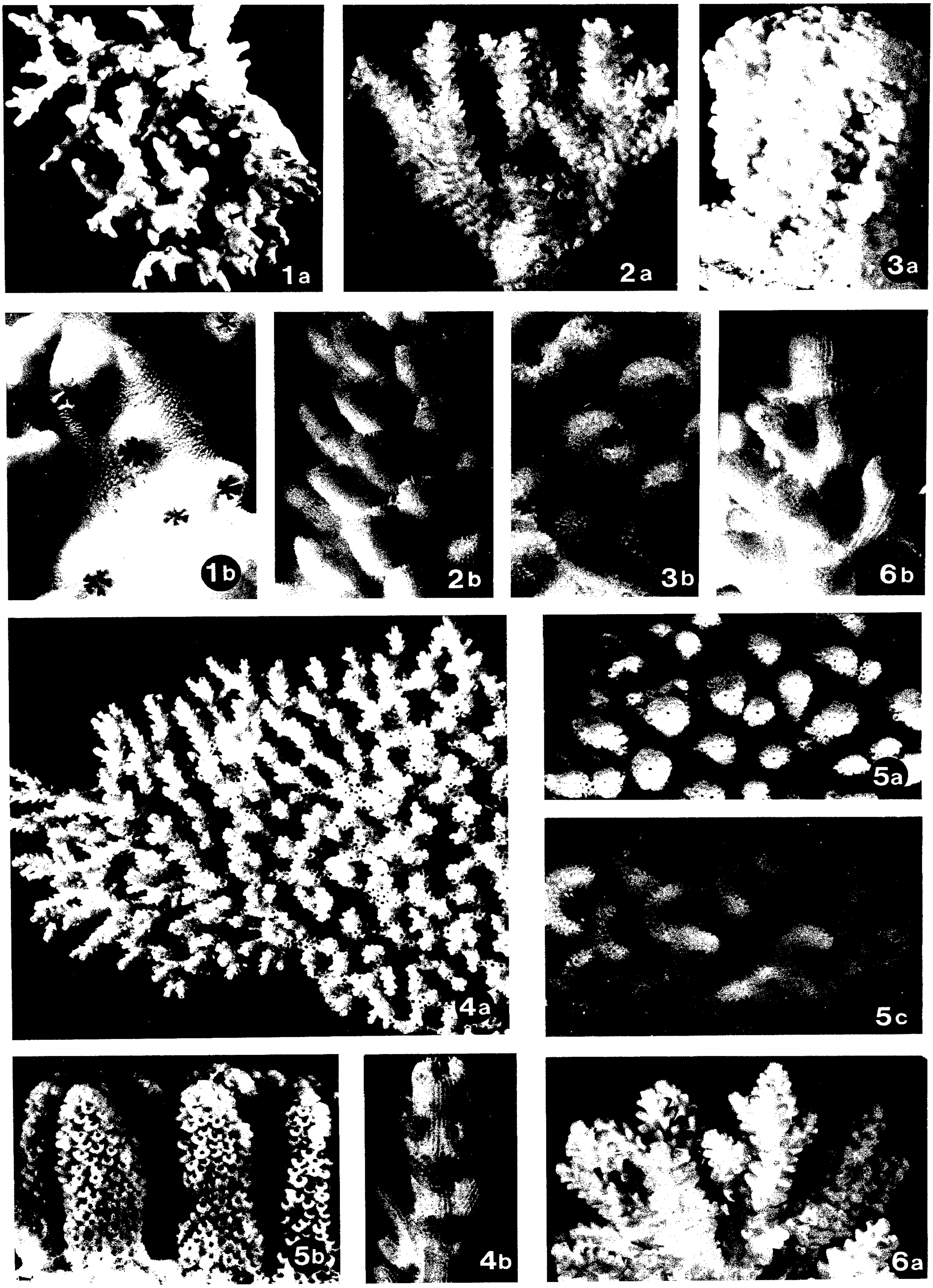
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Plate 4

Figs. 1a, b. *Acropora caroliniana* Nemenzo, 1976
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.
Figs. 2a, b. *Acropora clathrata* (Brook, 1891)
St. 1, Tr. 30, Kabira, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.
Figs. 3a, b. *Acropora cuneata* (Dana, 1846)
St. 1, Tr. 6, Kabira, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.
Figs. 4a, b. *Acropora cytherea* (Dana, 1846)
St. 1, Tr. 32, Kabira, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.
Figs. 5a-c. *Acropora digitifera* (Dana, 1846)
St. 3, Tr. 18, Shiraho, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×1, Fig. 5c, ×5.
Figs. 6a, b. *Acropora divaricata* (Dana, 1846)
St. 4, Tr. 3, Sesoko-jima, Okinawa.
Fig. 6a, ×1, Fig. 6b, ×5.

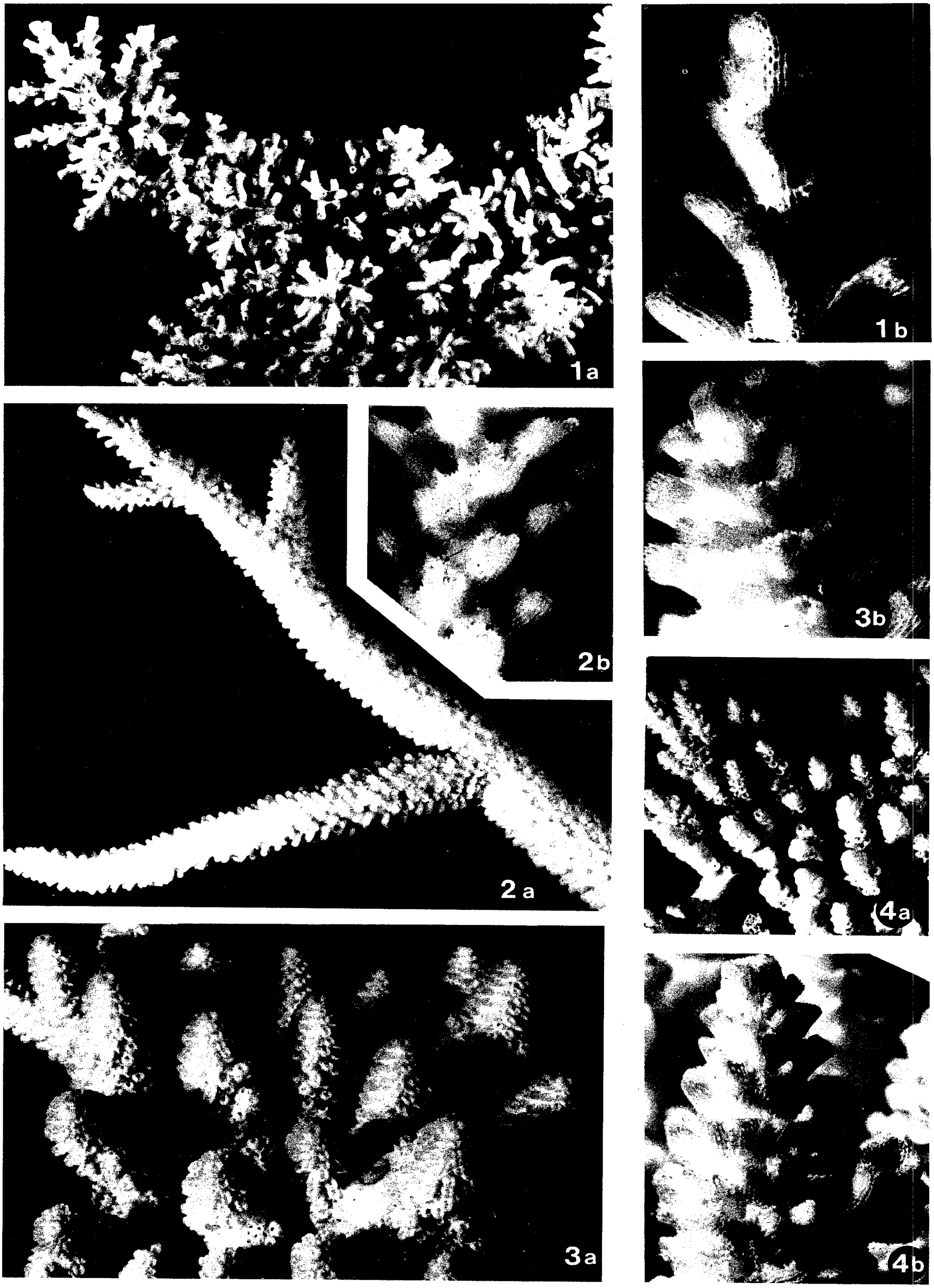
Plate 5

Figs. 1a, b. *Acropora echinata* (Dana, 1846)
St. 2, Tr. 3, Yonehara, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a, b. *Acropora formosa* (Dana, 1846)
St. 3, Shiraho, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×5.

Figs. 3a, b. *Acropora humilis* (Dana, 1846)
St. 4, Sesoko-jima, Okinawa.
Fig. 3a, ×1, Fig. 3b, ×5.

Figs. 4a, b. *Acropora hyacinthus* (Dana, 1846)
St. 3, Tr. 19, Shiraho, Ishigaki-jima.
Fig. 4a, ×1, Fig. 4b, ×5.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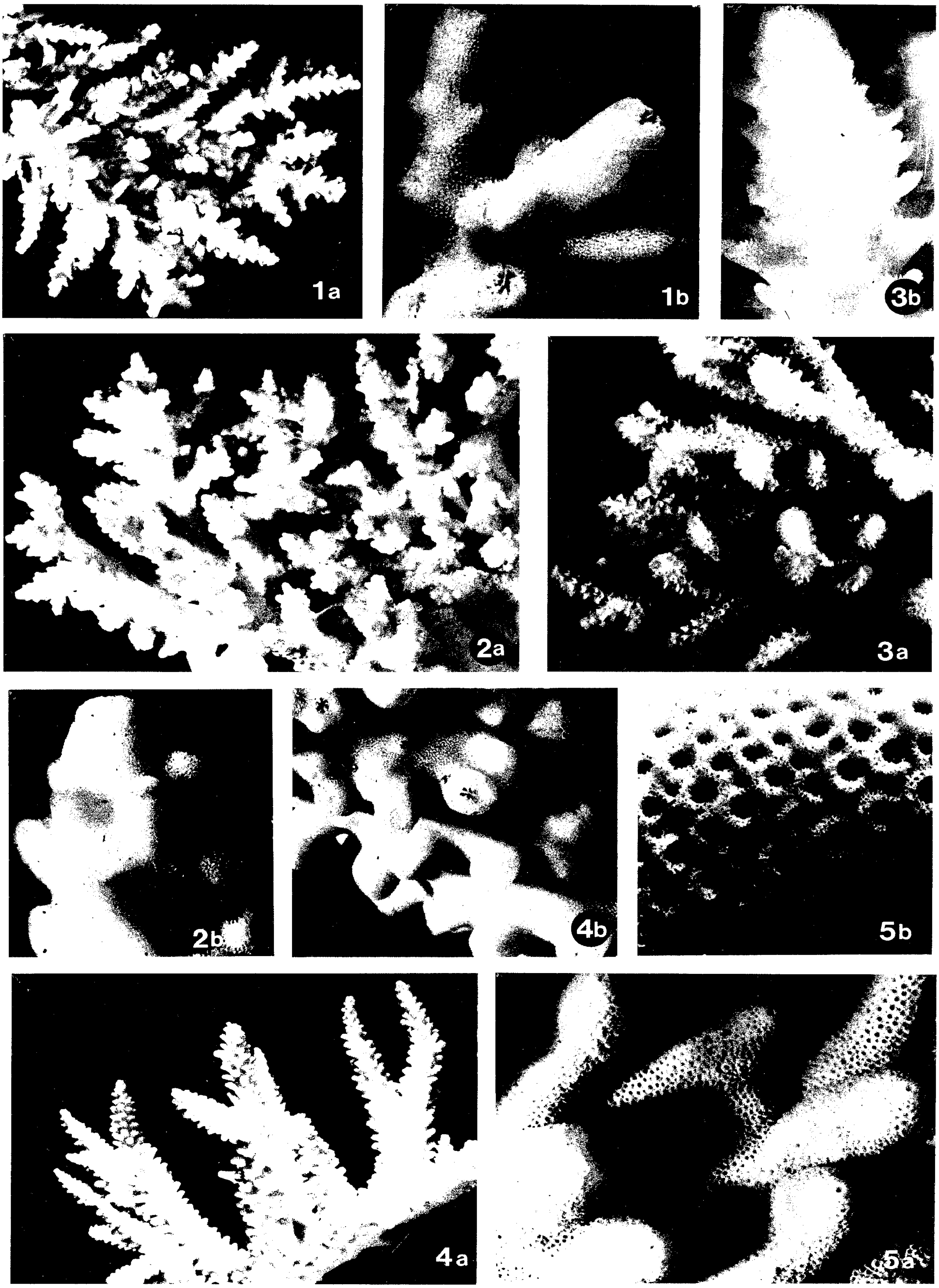
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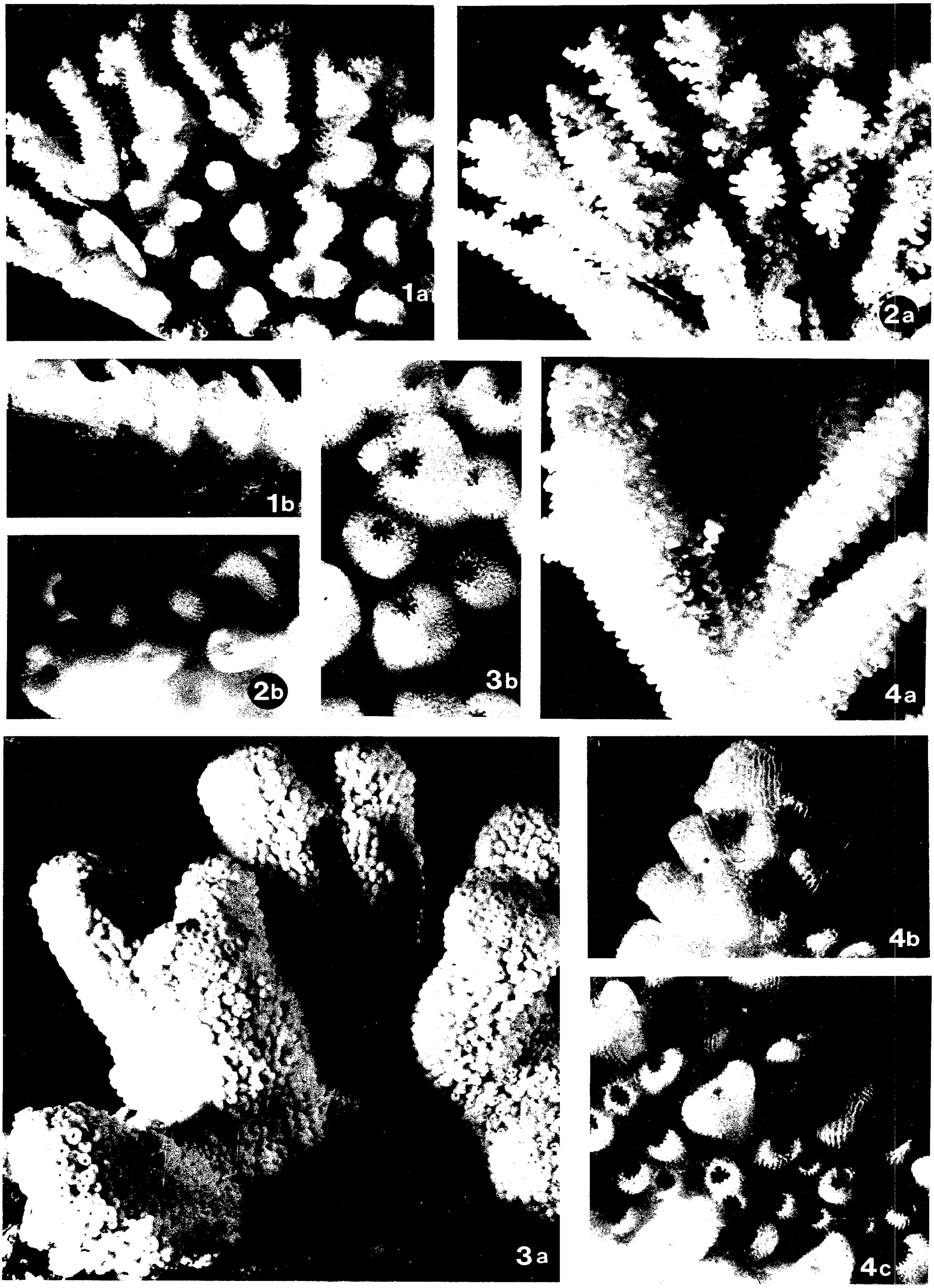
Plate 6

Figs. 1a, b. *Acropora longicyathus* (Edwards & Haime, 1860)
St. 1, Tr. 12, Kabira, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.
Figs. 2a, b. *Acropora loripes* (Brook, 1892)
St. 1, Tr. 30, Kabira, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×5.
Figs. 3a, b. *Acropora microcladose* (Ehrenberg, 1834)
St. 3, Tr. 8, Shiraho, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.
Figs. 4a, b. *Acropora microphthalma* (Verrill, 1869)
St. 3, Shiraho, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.
Figs. 5a, b. *Acropora monticulosa* (Brüggemann, 1879)
St. 1, Tr. 26, Kabira, Ishigaki-jima.
Fig. 5a, ×1, Fig. 5b, ×5.

Plate 7

Figs. 1a, b. *Acropora millepora* (Ehrenberg, 1834)
St. 4, Tr. 5, Sesoko-jima, Okinawa.
Fig. 1a, ×0.6,, Fig. 1b, ×5.
Figs. 2a, b. *Acropora nasuta* (Dana, 1846)
St. 3, Tr. 6, Shiraho, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×5.
Figs. 3a, b. *Acropora palifera* (Lamarck, 1816)
St. 3, Tr. 12, Shiraho, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×5.
Figs. 4a-c. *Acropora nobilis* (Dana, 1846)
St. 4, Tr. 2, Sesoko-jima, Okinawa.
Fig. 4a, ×1, Figs. 4b, c, ×5.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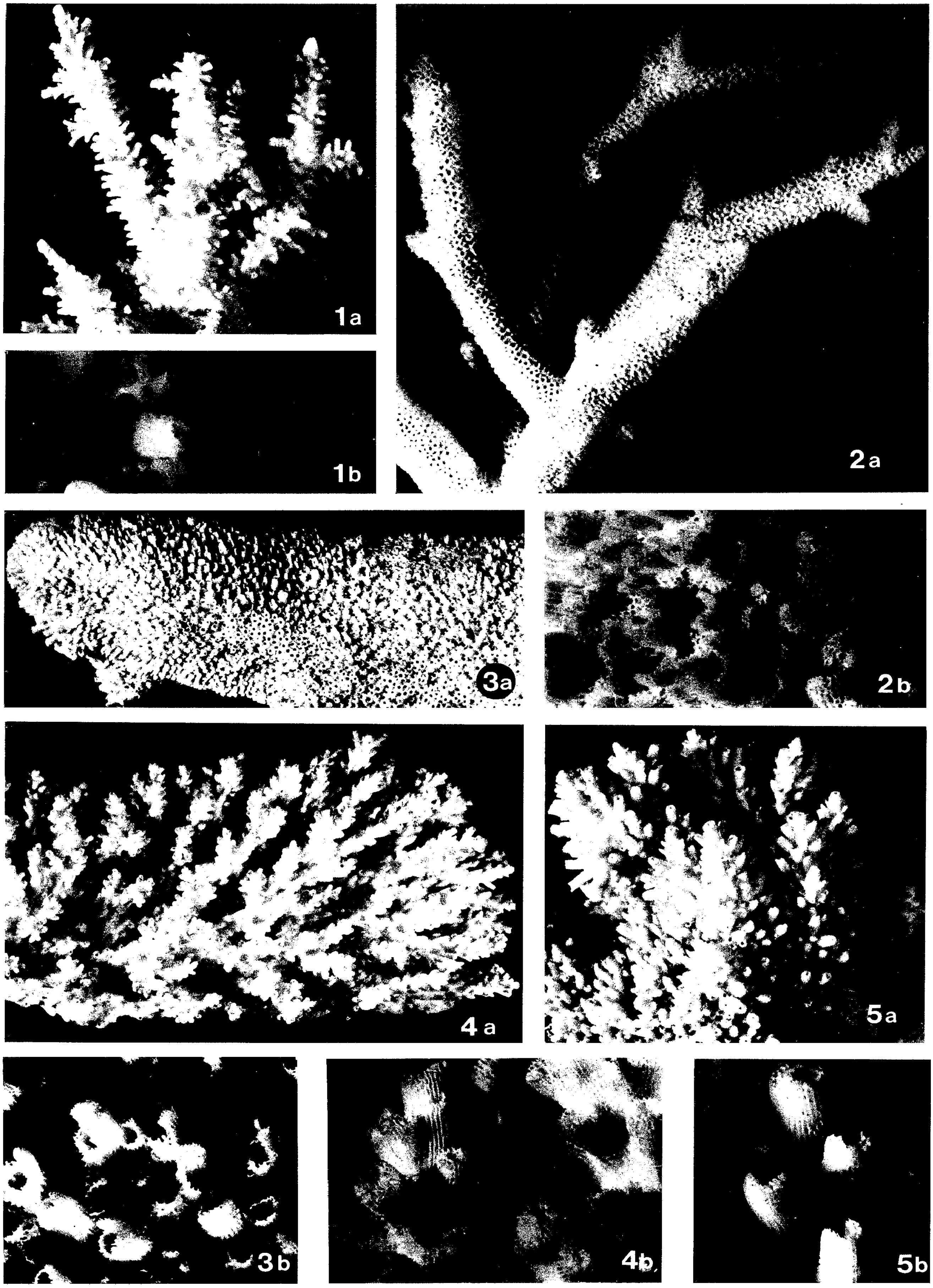
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Plate 8

Figs. 1a, b. *Acropora paniculata* Verrill, 1902
St. 1, Tr. 8, Kabira, Ishigaki-jima.
Fig. 1a, $\times 1$, Fig. 1b, $\times 5$.

Figs. 2a, b. *Acropora pulchra* (Brook, 1891)
St. 1, Tr. 20, Kabira, Ishigaki-jima.
Fig. 2a, $\times 0.67$, Fig. 2b, $\times 5$.

Figs. 3a, b. *Acropora palmerae* Wells, 1954
St. 1, Tr. 27, Kabira, Ishigaki-jima.
Fig. 3a, $\times 0.67$, Fig. 3b, $\times 5$.

Figs. 4a, b. *Acropora rambleri* (Bassett-Smith, 1890)
St. 1, Tr. 32, Kabira, Ishigaki-jima.
Fig. 4a, $\times 0.67$, Fig. 4b, $\times 5$.

Figs. 5a, b. *Acropora valida* (Dana, 1846)
St. 3, Tr. 19, Shiraho, Ishigaki-jima.
Fig. 5a, $\times 1$, Fig. 5b, $\times 5$.

Plate 9

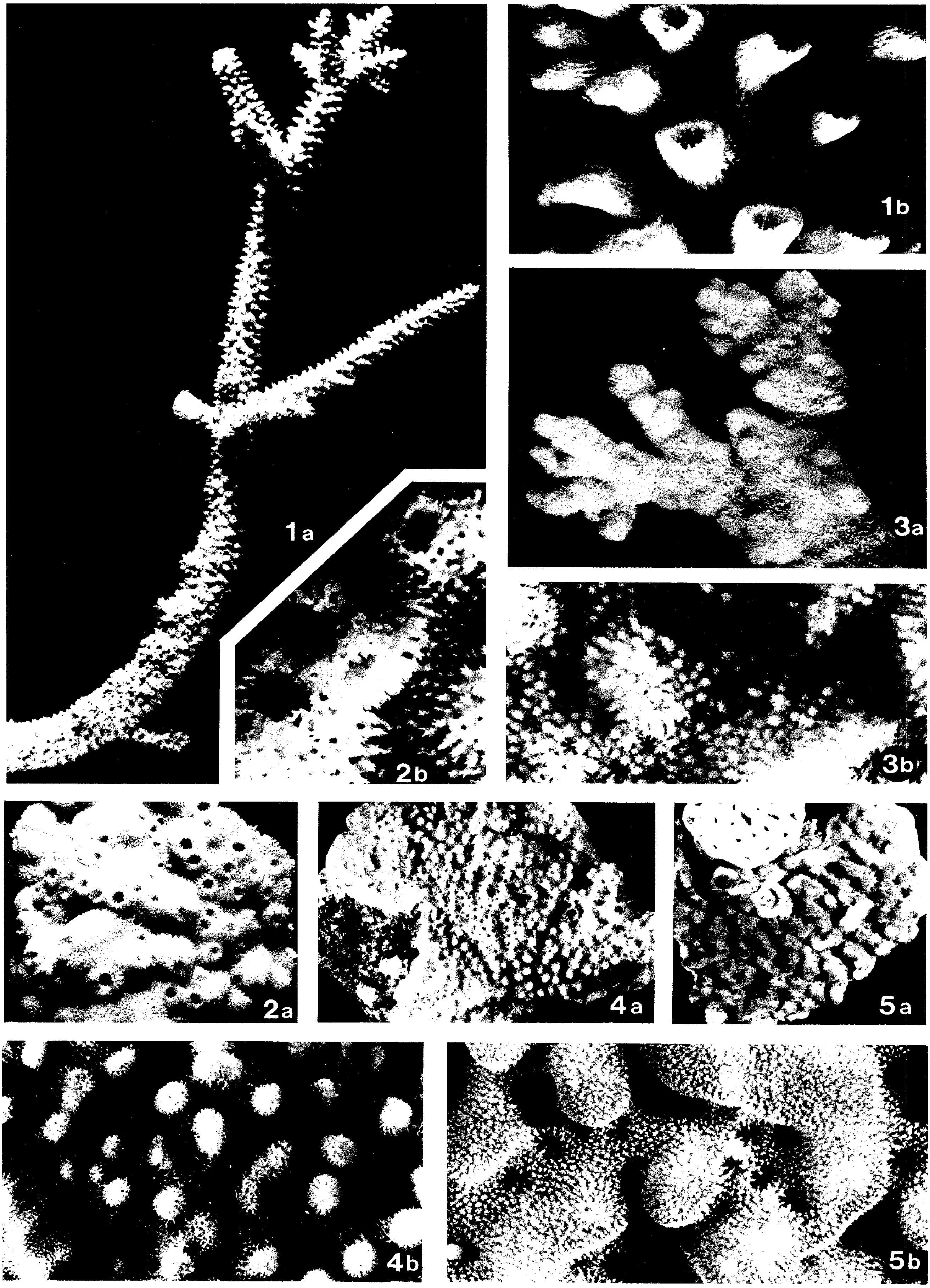
Figs. 1a, b. *Acropora valenciennesi* (Edwards & Haime, 1860)
St. 1, Tr. 11, Kabira, Ishigaki-jima.
Fig. 1a, ×0.5, Fig. 1b, ×5.

Figs. 2a, b. *Astreopora gracilis* Bernard, 1896
St. 1, Tr. 4, Kabira, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.

Figs. 3a, b. *Montipora cactus* Bernard, 1897
St. 3, Tr. 6, Shiraho, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×5.

Figs. 4a, b. *Montipora conicula* Wells, 1954
St. 4, Tr. 5, Sesoko-jima, Okinawa.
Fig. 4a, ×1, Fig. 4b, ×5.

Figs. 5a, b. *Montipora danae* Edwards & Haime, 1851
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.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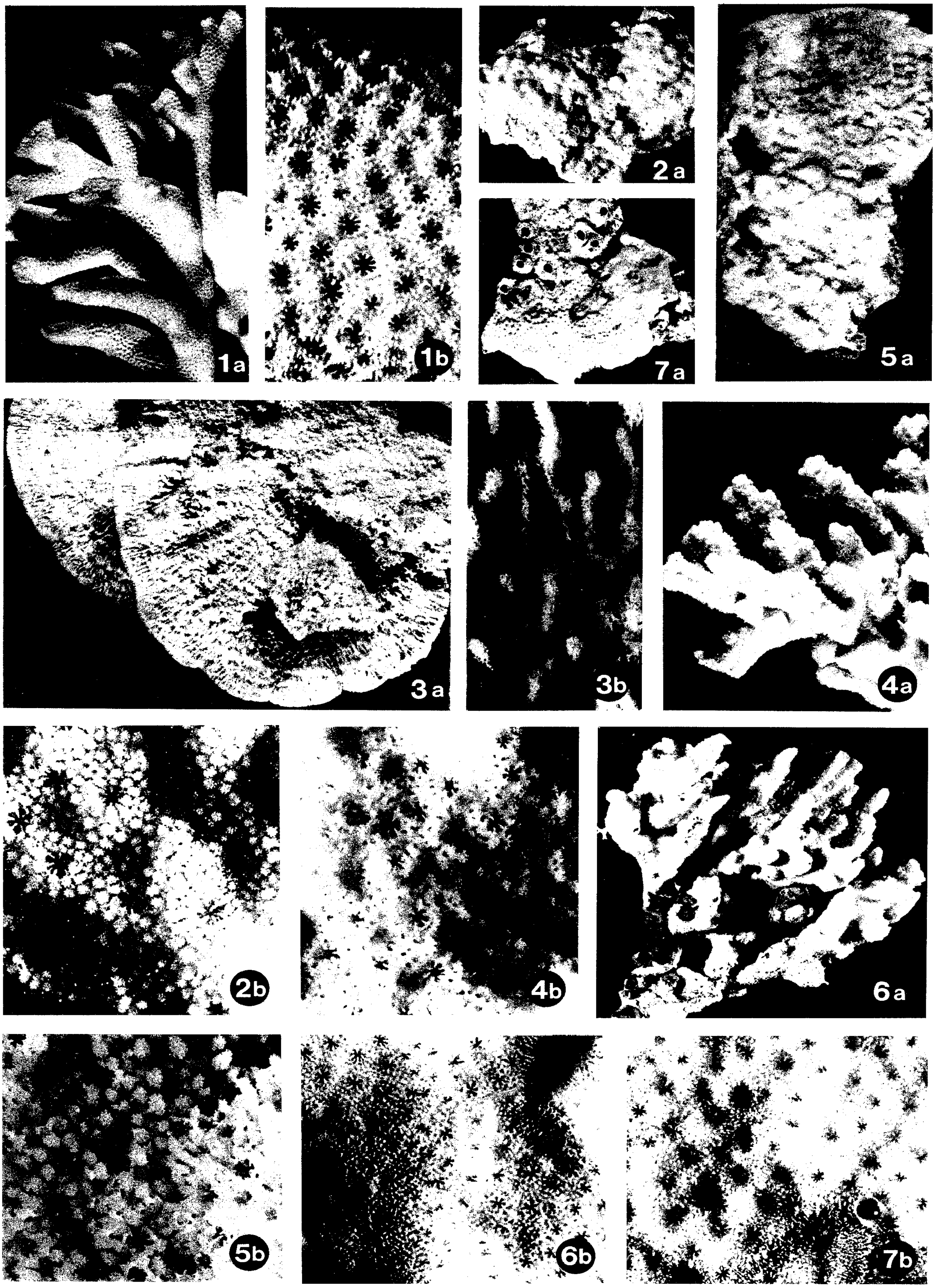
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Plate 10

Figs. 1a, b. *Montipora digitata* (Dana, 1846)
St. 2, Tr. 1, Yonehara, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a, b. *Montipora efflorescens* Bernard, 1897
St. 1, Tr. 33, Kabira, Ishigaki-jima
Fig. 2a, ×0.67, Fig. 2b, ×5.

Figs. 3a, b. *Montipora foliosa* (Pallas, 1766)
St. 1, Tr. 21, Kabira, Ishigaki-jima.
Fig. 3a, ×0.5, Fig. 3b, ×5.

Figs. 4a, b. *Montipora hispida* (Dana, 1846)
St. 3, Tr. 4, Shiraho, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.

Figs. 5a, b. *Montipora informis* Bernard, 1897
Kabira Cove, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.

Figs. 6a, b. *Montipora mollis* Bernard, 1897
St. 1, Tr. 22, Kabira, Ishigaki-jima.
Fig. 6a, ×0.67, Fig. 6b, ×5.

Figs. 7a, b. *Montipora spongodes* Bernard, 1897
St. 4, Tr. 5, Sesoko-jima, Okinawa.
Fig. 7a, ×0.67, Fig. 7b, ×5.

Plate 11

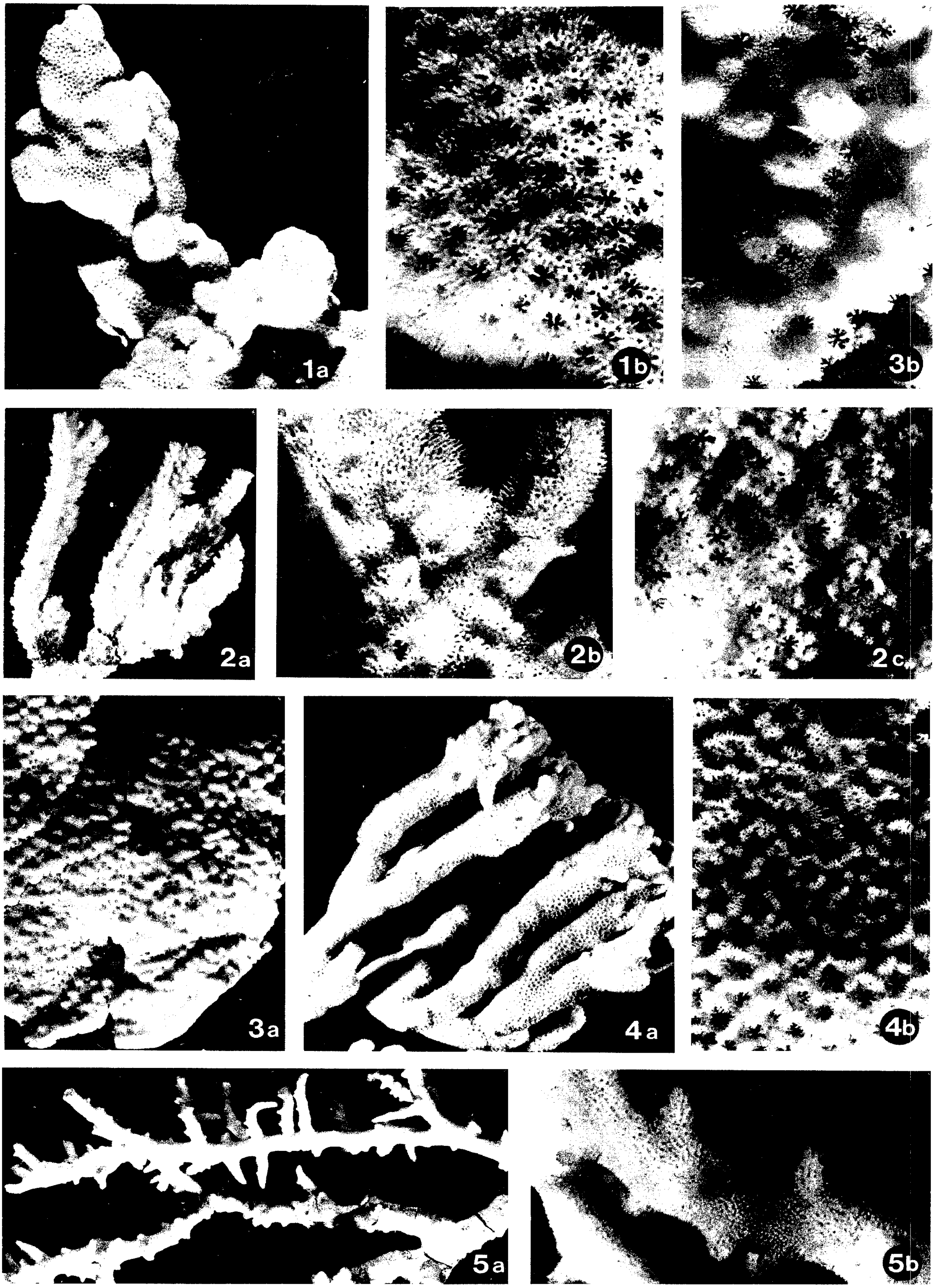
Figs. 1a, b. *Montipora spumosa* (Lamarck, 1816)
St. 1, Tr. 9, Kabira, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a-c. *Montipora stellata* Bernard, 1897
St. 2, Tr. 2, Yonehara, Ishigaki-jima.
Fig. 2a, ×0.67, Figs. 2a, c, ×5.

Figs. 3a, b. *Montipora verrucosa* (Lamarck, 1816)
St. 1, Tr. 32, Kabira, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.

Figs. 4a, b. *Montipora* sp. A
St. 3, Tr. 13, Shiraho, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.

Figs. 5a, b. *Anacropora spinosa* Rehberg, 1892
Kabira Cove, Ishigaki-jima.
Fig. 5a, ×1, Fig. 5b, ×5.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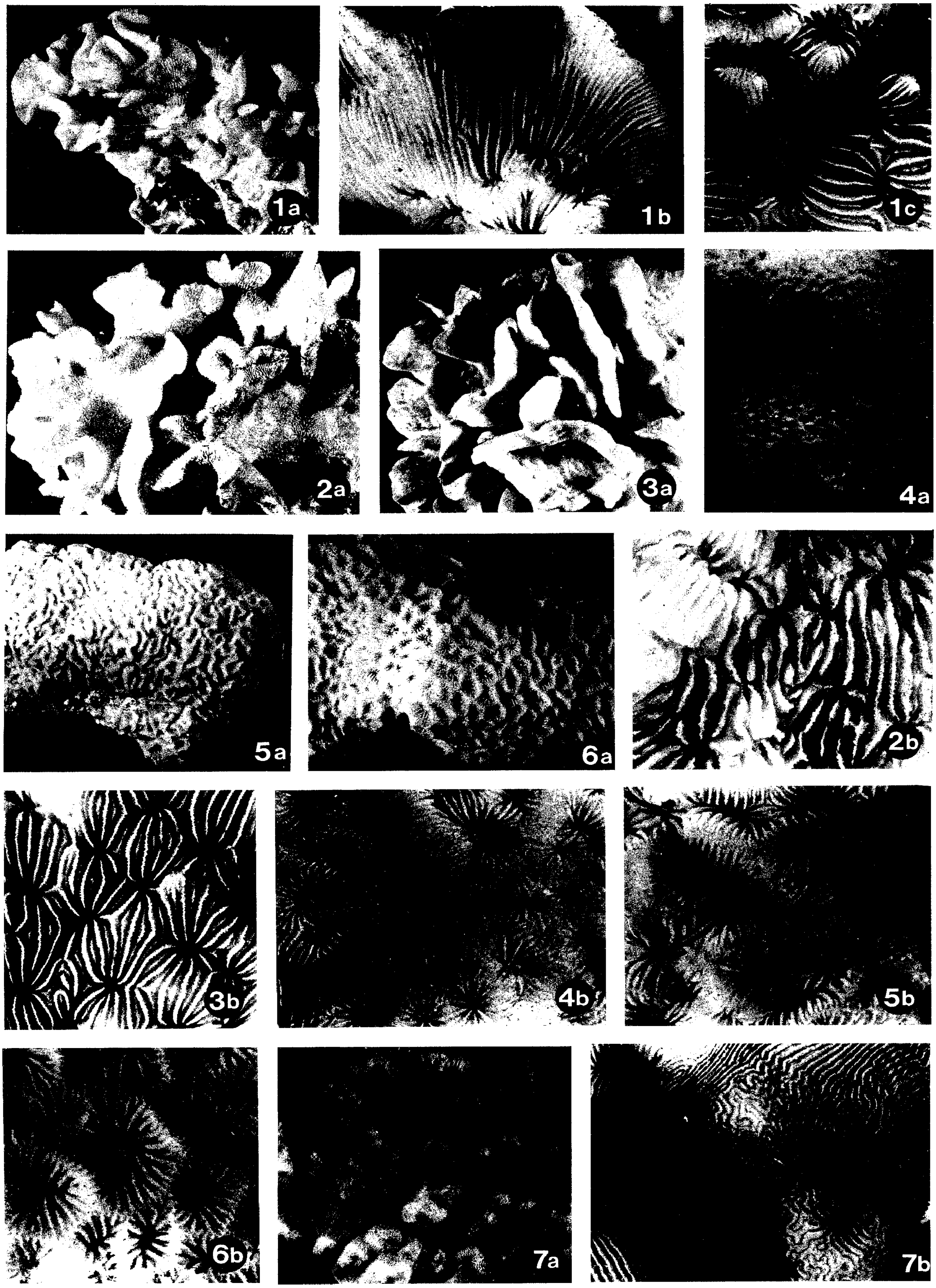
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Plate 12

Figs. 1a-c. *Pavona divaricata* Lamarck, 1816
St. 1, Tr. 21, Kabira, Ishigaki-jima.
Fig. 1a, $\times 1$, Figs. 1b, c, $\times 5$.

Figs. 2a, b. *Pavona decussata* (Dana, 1846)
St. 1, Tr. 18, Kabira, Ishigaki-jima.
Fig. 2a, $\times 0.67$, Fig. 2b, $\times 5$.

Figs. 3a, b. *Pavona frondifera* Lamarck, 1816
St. 1, Tr. 18, Kabira, Ishigaki-jima.
Fig. 3a, $\times 0.67$, Fig. 3b, $\times 5$.

Figs. 4a, b. *Pavona minuta* Wells, 1954
Kabira Pass, Ishigaki-jima.
Fig. 4a, $\times 1$, Fig. 4b, $\times 5$.

Figs. 5a, b. *Pavona varians* Verrill, 1864
St. 1, Tr. 15, Kabira, Ishigaki-jima.
Fig. 5a, $\times 0.67$, Fig. 5b, $\times 5$.

Figs. 6a, b. *Pavona venosa* (Ehrenberg, 1834)
St. 1, Tr. 2, Kabira, Ishigaki-jima.
Fig. 6a, $\times 1$, Fig. 6b, $\times 5$.

Figs. 7a, b. *Leptoseris hawaiiensis* Vaughan, 1907
Gamo-saki, Kasari, Amami-oshima.
Fig. 7a, $\times 1$, Fig. 7b, $\times 5$.

Plate 13

Figs. 1a, b. *Leptoseris mycetoseroides* Wells, 1954
Yoan, Kasari, Amami-oshima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a, b. *Leptoseris scabra* Vaughan, 1907
Gamo-saki, Kasari, Amami-oshima.
Fig. 2a, ×1, Fig. 2b, ×5.

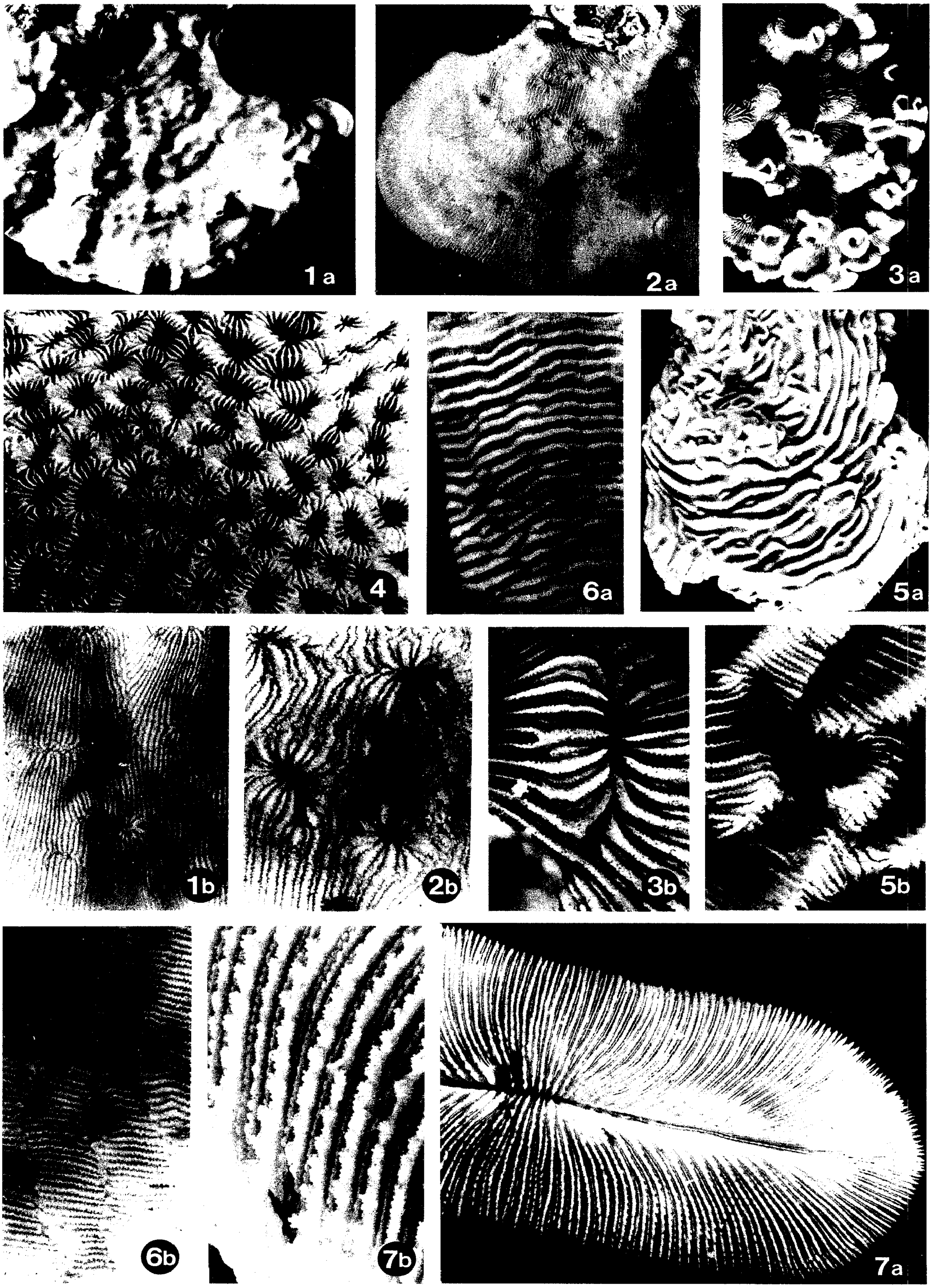
Figs. 3a, b. *Leptoseris scabra* Vaughan, 1907
Kabira Cove, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×5.

Fig. 4. *Coeloseris mayeri* Vaughan, 1918
St. 2, Tr. 4, Yonehara, Ishigaki-jima. ×2.

Figs. 5a, b. *Pachyseris rugosa* (Lamarck, 1801)
St. 1, Tr. 18, Kabira, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.

Figs. 6a, b. *Pachyseris speciosa* (Dana, 1846)
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 6a, ×1, Fig. 6b, ×5.

Figs. 7a, b. *Fungia echinata* (Pallas, 1766)
St. 1, Kabira, Ishigaki-jima.
Fig. 7a, ×0.5, Fig. 7b, ×2.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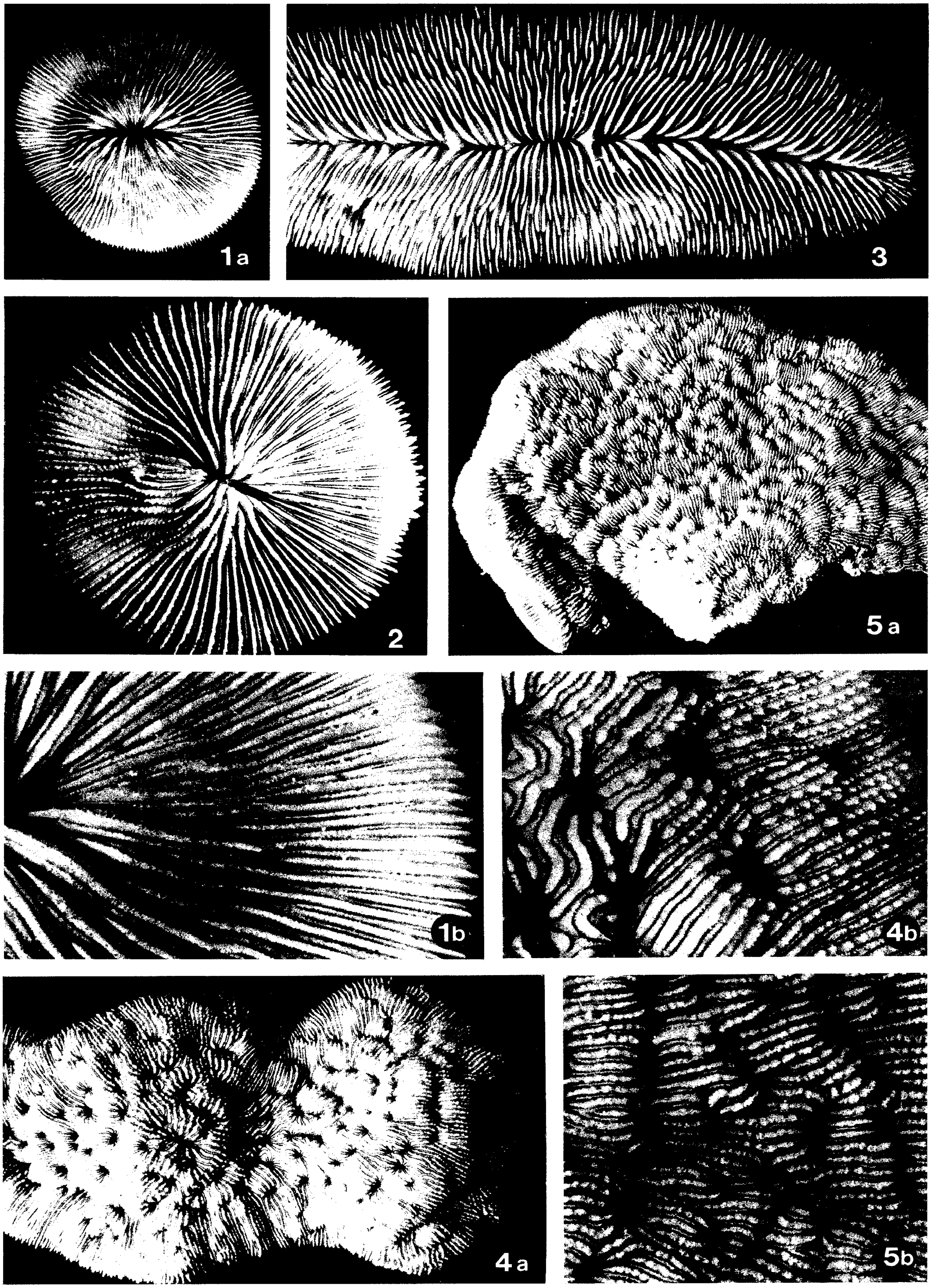
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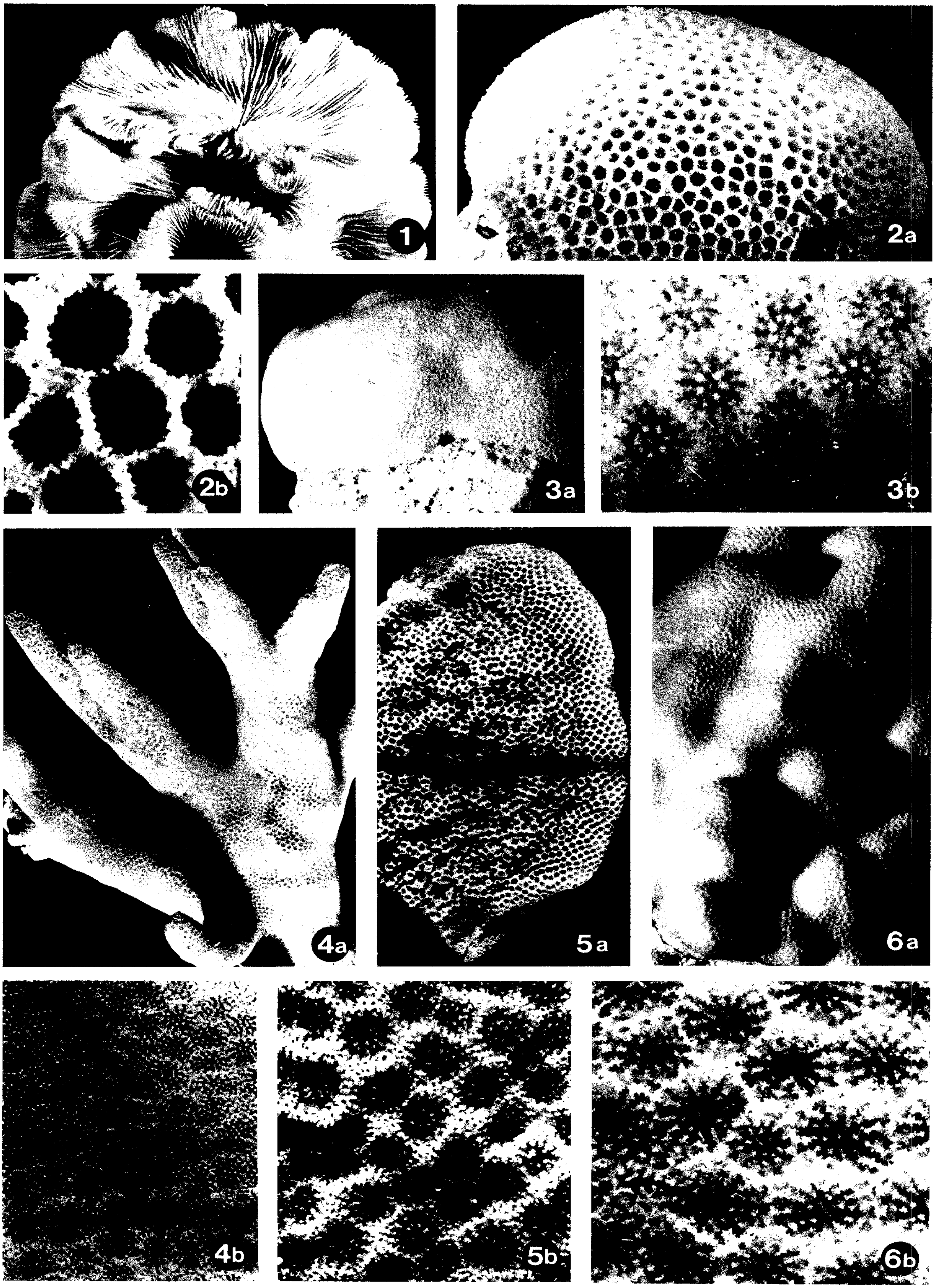
Plate 14

Figs. 1a, b. *Fungia granulosa* Klunzinger, 1879
Yoan, Kasari, Amami-oshima.
Fig. 1a, $\times 0.5$, Fig. 1b, $\times 2$.
Fig. 2. *Fungia horrida* Dana, 1846
Kabira Cove, Ishigaki-jima. $\times 0.5$.
Fig. 3. *Herpolitha limax* (Houttuyn, 1772)
Tachigami, Kasari, Amami-oshima. $\times 0.67$.
Figs. 4a, b. *Sandalolitha robusta* (Quelch, 1886)
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 4a, $\times 0.5$, Fig. 4b, $\times 2$.
Figs. 5a, b. *Podabacia crustacea* (Pallas, 1766)
Gamo-saki, Kasari, Amami-oshima.
Fig. 5a, $\times 0.67$, Fig. 5b, $\times 2$.

Plate 15

Fig. 1. *Lithophyllon edwardsi* (Rousseau, 1854)
Tatsugo, Amami-oshima. ×0.67.
Figs. 2a, b. *Goniopora gracilis* (Bassett-Smith, 1890)
St. 3, Tr. 4, Shiraho, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.
Figs. 3a, b. *Porites australiensis* Vaughan, 1918
St. 1, Kabira, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×10.
Figs. 4a, b. *Porites cylindrica* Dana, 1846
Kabira Cove, Ishigaki-jima.
Fig. 4a, ×0.67, Fig. 4b, ×5.
Figs. 5a, b. *Porites lichen* Dana, 1846
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.
Figs. 6a, b. *Porites lobata* Dana, 1846
St. 1, Kabira, Ishigaki-jima.
Fig. 6a, ×0.67, Fig. 6b, ×10.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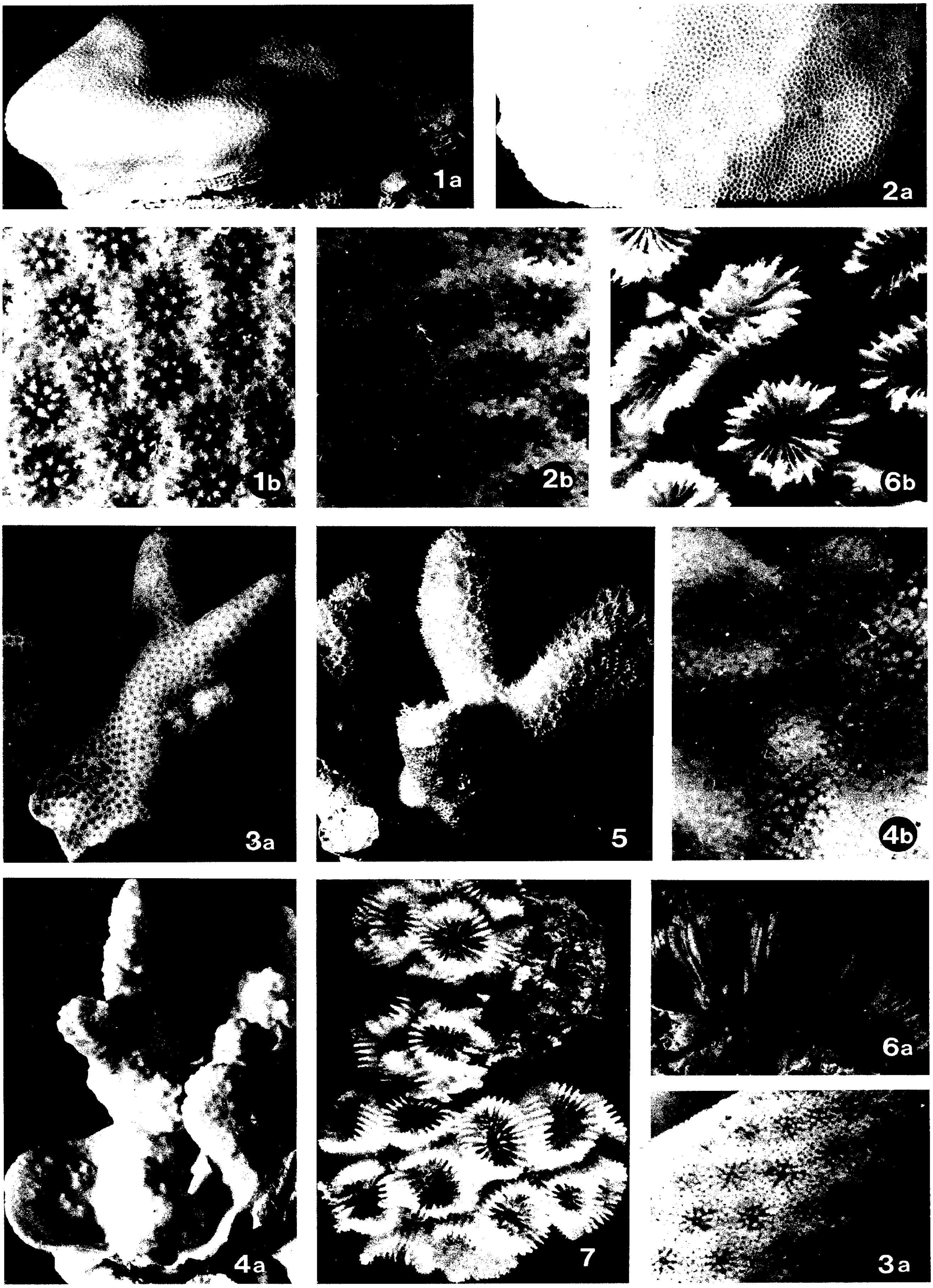
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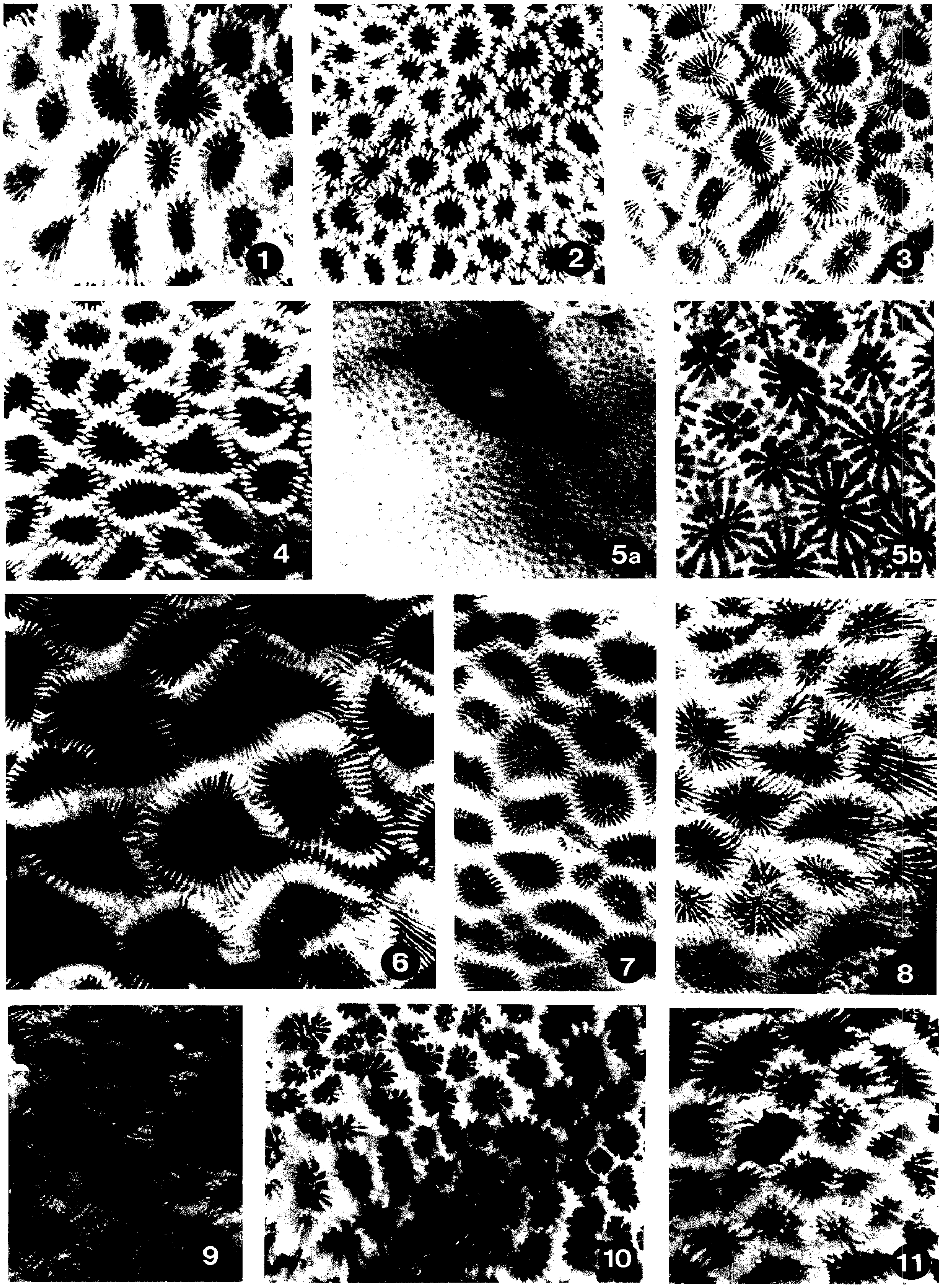
Plate 16

Figs. 1a, b. *Porites lutea* Edwards & Haime, 1860
St. 1, Kabira, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×10.
Figs. 2a, b. *Porites mayeri* Vaughan, 1918
St. 1, Kabira, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×10.
Figs. 3a, b. *Porites nigrescens* Dana, 1848
St. 1, Tr. 12, Kabira, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.
Figs. 4a, b. *Porites rus* (Forskål, 1775)
St. 1, Tr. 31, Kabira, Ishigaki-jima.
Fig. 4a, ×1, Fig. 4b, ×10.
Fig. 5. *Alveopora verrilliana* Dana, 1872
Yoan, Kasari, Amami-oshima. ×1.
Figs. 6a, b. *Caulastrea furcata* Dana, 1846
St. 1, Kabira, Ishigaki-jima.
Fig. 6a, ×1, Fig. 6b, ×2.
Fig. 7. *Barabattoia amicorum* (Edwards & Haime, 1850)
Yoan, Kasari, Amami-oshima. ×1.

Plate 17

Fig. 1. *Favia favus* (Forskål, 1775)
St. 1, Tr. 22, Kabira, Ishigaki-jima. ×1.
Fig. 2. *Favia matthaii* Vaughan, 1918
St. 1, Tr. 31, Kabira, Ishigaki-jima. ×1.
Fig. 3. *Favia pallida* (Dana, 1846)
St. 1, Tr. 5, Kabira, Ishigaki-jima. ×1.
Fig. 4. *Favia speciosa* (Dana, 1846)
St. 4, Tr. 3, Sesoko-jima, Okinawa. ×1.
Figs. 5a, b. *Favia stelligera* (Dana, 1846)
St. 1, Tr. 30, Kabira, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.
Fig. 6. *Favia* sp. 2 *in* Veron *et al.*, 1977
Yoan, Kasari, Amami-oshima. ×1.
Fig. 7. *Favites abdita* (Ellis & Solander, 1786)
St. 1, Tr. 31, Kabira, Ishigaki-jima. ×1.
Fig. 8. *Favites flexuosa* (Dana, 1846)
Yoan, Kasari, Amami-oshima. ×1.
Fig. 9. *Favites halicora* (Ehrenberg, 1834)
St. 4, Tr. 5, Sesoko-jima, Okinawa. ×1.
Fig. 10. *Favites pentagona* (Esper, 1794)
St. 4, Tr. 5, Sesoko-jima, Okinawa. ×1.
Fig. 11. *Goniastrea aspera* Verrill, 1865
St. 2, Tr. 5, Yonehara, Ishigaki-jima. ×2.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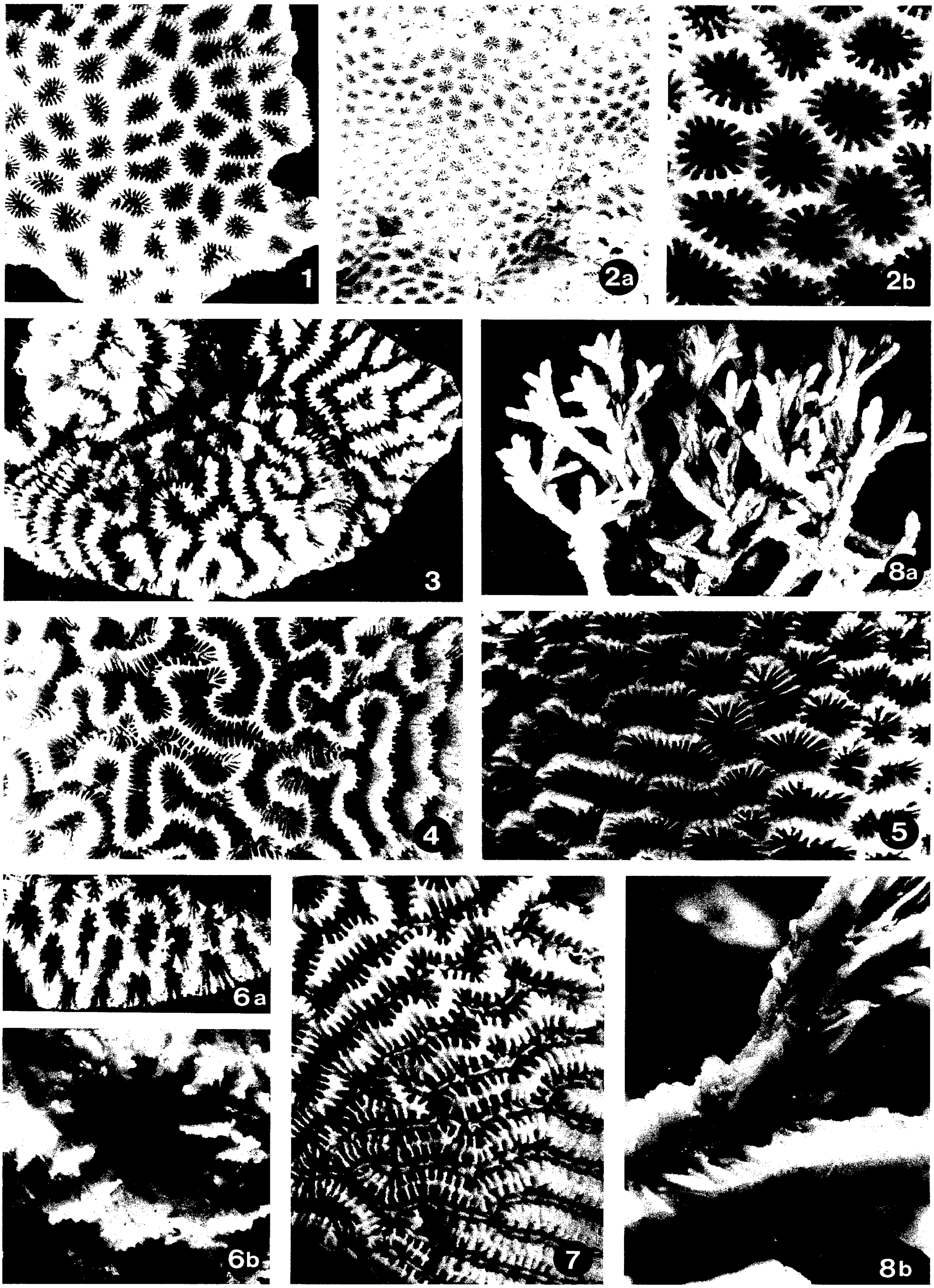
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Plate 18

Fig. 1. *Goniastrea pectinata* (Ehrenberg, 1834)
St. 1, Tr. 30, Kabira, Ishigaki-jima. ×1.
Figs. 2a, b. *Goniastrea retiformis* (Lamarck, 1816)
St. 1, Tr. 26, Kabira, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.
Fig. 3. *Platygyra lamellina* (Ehrenberg, 1834)
St. 4, Tr. 5, Sesoko-jima, Okinawa. ×1.
Fig. 4. *Platygyra daedalea* (Ellis & Solander, 1786)
St. 4, Sesoko-jima, Okinawa. ×1.
Fig. 5. *Platygyra sinensis* (Edwards & Haime, 1849)
St. 2, Tr. 6, Yonehara, Ishigaki-jima. ×2.
Figs. 6a, b. *Platygyra pini* Chevalier, 1975
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 6a, ×1, Fig. 6b, ×5.
Fig. 7. *Leptoria phrygia* (Ellis & Solander, 1786)
St. 2, Tr. 6, Yonehara, Ishigaki-jima. ×2.
Figs. 8a, b. *Hydnophora rigida* (Dana, 1846)
St. 1, Tr. 21, Kabira, Ishigaki-jima.
Fig. 8a, ×0.67, Fig. 8b, ×5.

Plate 19

Fig. 1. *Hydnophora microconos* (Lamarck, 1816)
St. 3, Shiraho, Ishigaki-jima. ×2.

Fig. 2. *Montastrea annuligera* (Edwards & Haime, 1849)
St. 1, Tr. 22, Kabira, Ishigaki-jima. ×2.

Fig. 3. *Montastrea curta* (Dana, 1846)
St. 1, Tr. 32, Kabira, Ishigaki-jima. ×2.

Fig. 4. *Montastrea valenciennesi* (Edwards & Haime, 1848)
St. 2, Tr. 1, Yonehara, Ishigaki-jima. ×2.

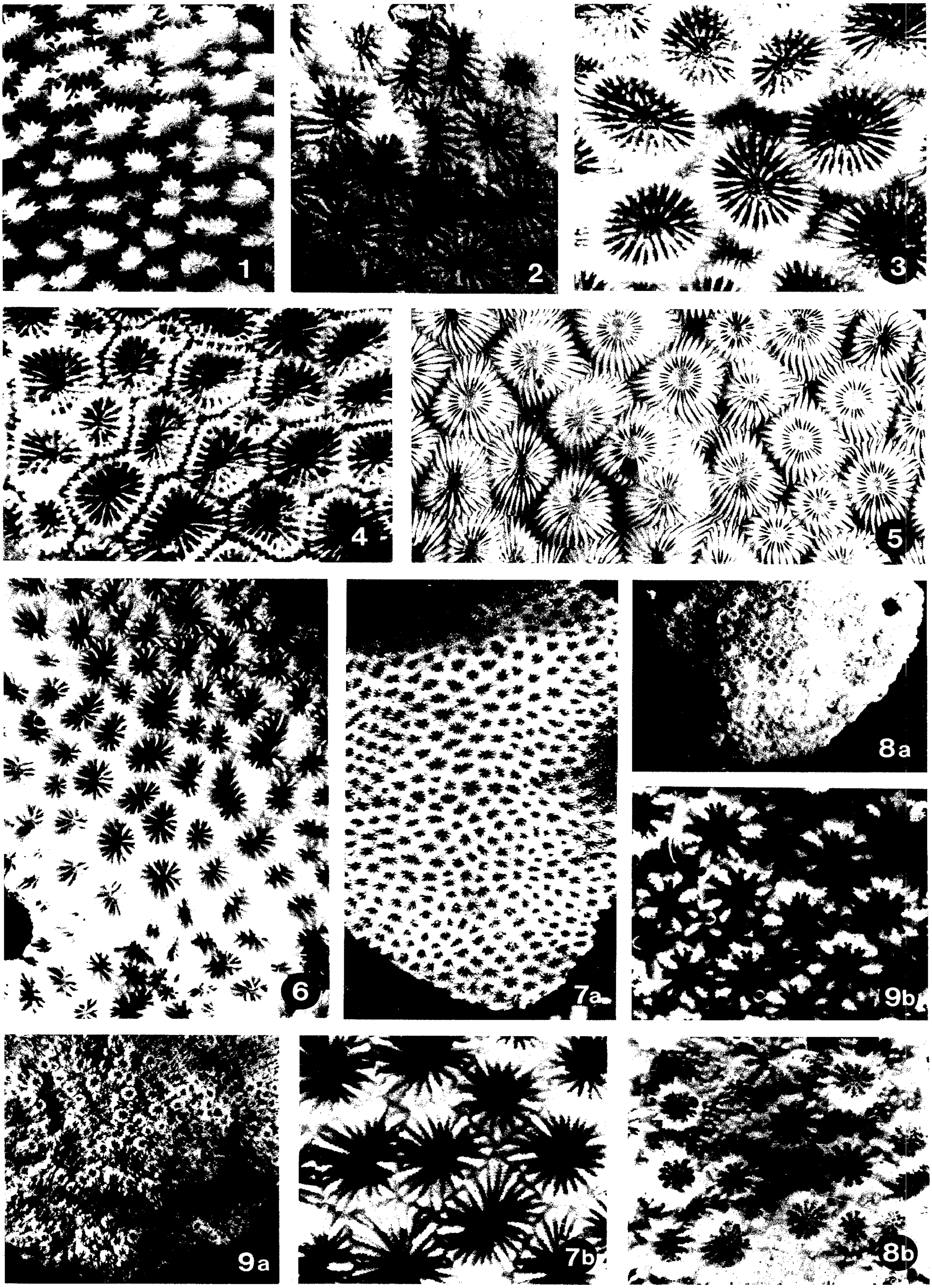
Fig. 5. *Diploastrea heliopora* (Lamarck, 1816)
St. 4, Sesoko-jima, Okinawa. ×1.

Fig. 6. *Leptastrea purpurea* (Dana, 1846)
St. 4, Sesoko-jima, Okinawa. ×2.

Figs. 7a, b. *Leptastrea transversa* Klunzinger, 1879
St. 1, Tr. 33, Kabira, Ishigaki-jima.
Fig. 7a, ×1, Fig. 7a, ×5.

Figs. 8a, b. *Cyphastrea chalcidicum* (Forskål, 1775)
St. 1, Tr. 4, Kabira, Ishigaki-jima.
Fig. 8a, ×0.67, Fig. 8b, ×5.

Figs. 9a, b. *Cyphastrea microphthalma* (Lamarck, 1816)
St. 1, Kabira, Ishigaki-jima.
Fig. 9a, ×0.67, Fig. 9b, ×5.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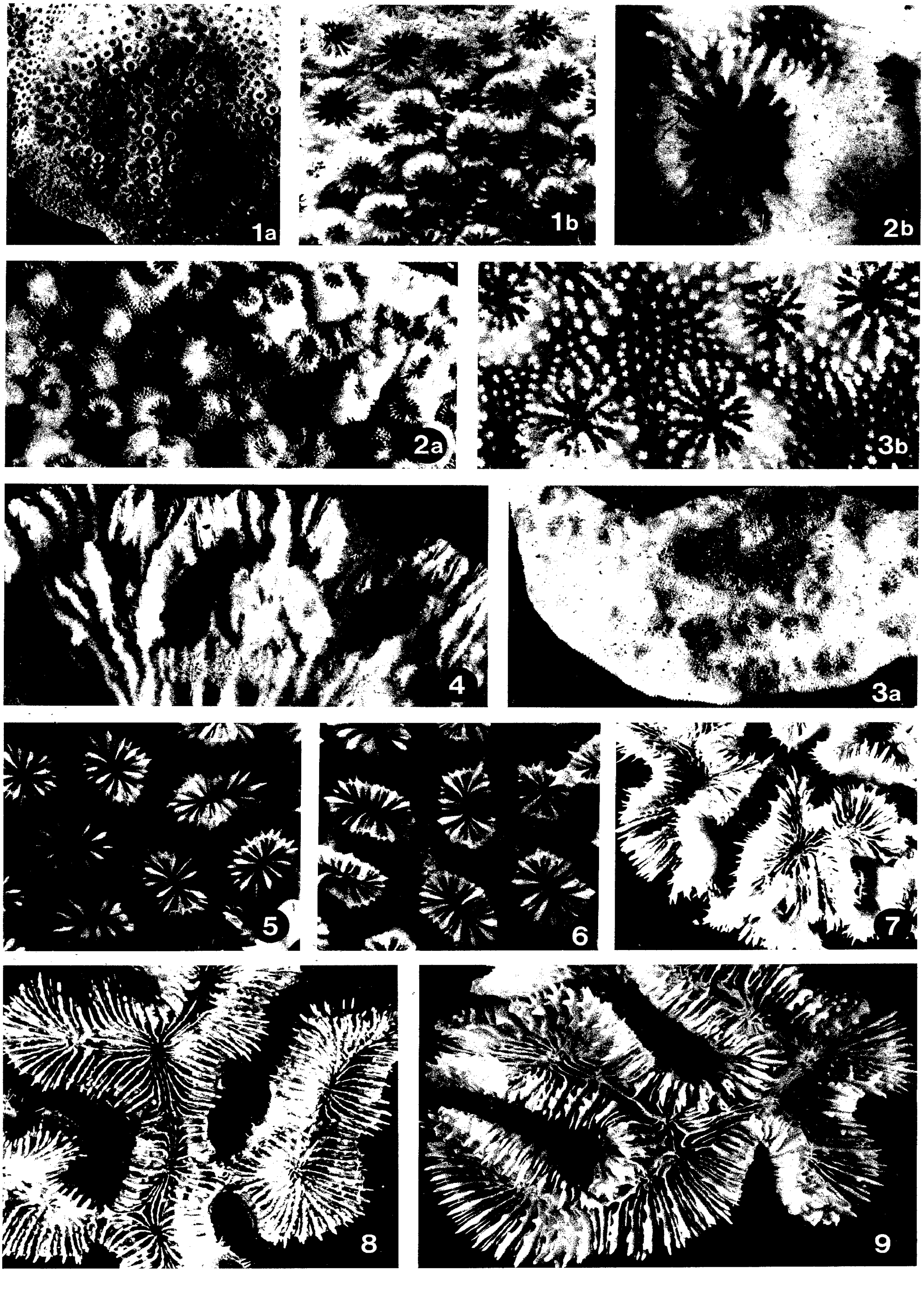
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Plate 20

Figs. 1a, b. *Cyphastrea serailia* (Forskål, 1775)
St. 3, Shiraho, Ishigaki-jima.
Fig. 1a, ×0.67, Fig. 1b, ×5.

Figs. 2a, b. *Echinopora hirsutissima* Edwards & Haime, 1849
St. 3, Tr. 19, Shiraho, Ishigaki-jima.
Fig. 2a, ×0.67, Fig. 2b, ×5.

Figs. 3a, b. *Echinopora lamellosa* (Esper, 1795)
St. 1, Tr. 30, Kabira, Ishigaki-jima.
Fig. 3a, ×1, Fig. 3b, ×5.

Fig. 4. *Merulina ampliata* (Ellis & Solander, 1786)
St. 1, Tr. 11, Kabira, Ishigaki-jima. ×1.

Fig. 5. *Galaxea astreata* (Lamarck, 1816)
St. 1, Tr. 13, Kabira, Ishigaki-jima. ×2.

Fig. 6. *Galaxea fascicularis* (Linnaeus, 1767)
St. 1, Tr. 16, Kabira, Ishigaki-jima. ×2.

Fig. 7. *Lobophyllia corymbosa* (Forskål, 1775)
Kabira Cove, Ishigaki-jima. ×0.67.

Fig. 8. *Lobophyllia hemprichii* (Ehrenberg, 1834)
St. 1, Tr. 33, Kabira, Ishigaki-jima. ×0.67.

Fig. 9. *Lobophyllia pachysepta* Chevalier, 1975
Yoan, Kasari, Amami-oshima. ×0.67.

Plate 21

Fig. 1. *Symphyllia recta* (Dana, 1846)
St. 1, Tr. 29, Kabira, Ishigaki-jima. ×1.
Fig. 2. *Oxypora lacera* (Verrill, 1864)
St. 1, Tr. 32, Kabira, Ishigaki-jima. ×2.
Fig. 3. *Echinophyllia aspera* (Ellis & Solander, 1786)
St. 1, Tr. 32, Kabira, Ishigaki-jima. ×0.67.
Fig. 4. *Mycedium elephantotus* (Pallas, 1766)
St. 1, Tr. 31, Kabira, Ishigaki-jima. ×1.
Fig. 5. *Pectinia lactuca* (Pallas, 1766)
St. 1, Tr. 31, Kabira, Ishigaki-jima. ×0.67.
Fig. 6. *Euphyllia fimbriata* (Spengler, 1799)
St. 1, Tr. 32, Kabira, Ishigaki-jima. ×0.67.
Fig. 7. *Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821)
St. 1, Tr. 21, Kabira, Ishigaki-jima. ×1.
Fig. 8. *Euphyllia* sp. A
St. 1, Tr. 31, Kabira, Ishigaki-jima. ×0.67.
Fig. 9. *Plerogyra sinuosa* (Dana, 1846)
Kabira Pass, Ishigaki-jima. ×0.67.


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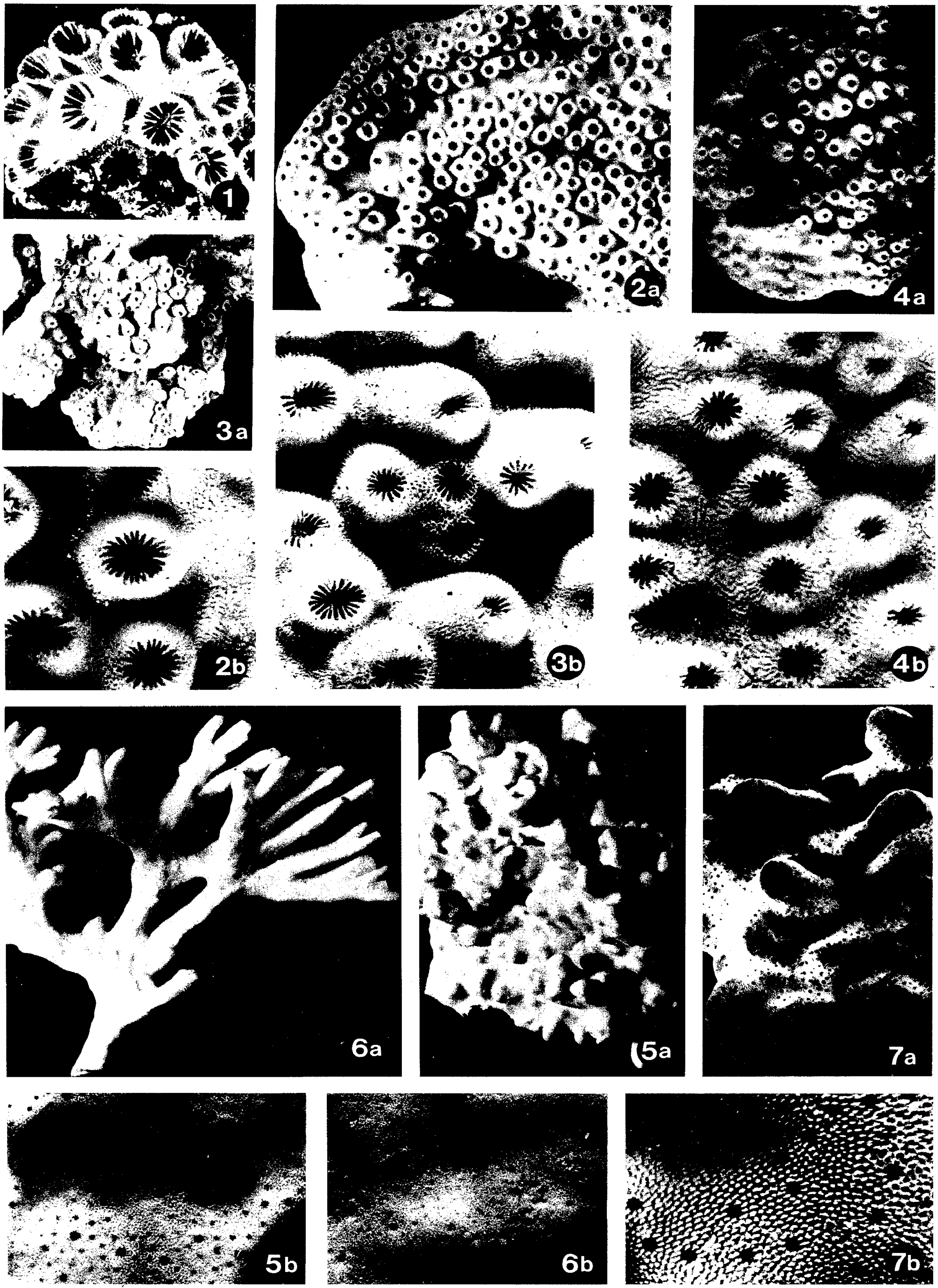
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Plate 22

Fig. 1. *Tubastraea aurea* (Quoy & Gaimard, 1833)
St. 4, Sesoko-jima, Okinawa. ×1.

Figs. 2a, b. *Turbinaria bifrons* Brüggemann, 1877
St. 1, Tr. 11, Kabira, Ishigaki-jima.
Fig. 2a, ×1, Fig. 2b, ×5.

Figs. 3a, b. *Turbinaria mesenterina* (Lamarck, 1816)
St. 1, Tr. 20, Kabira, Ishigaki-jima.
Fig. 3a, ×0.67, Fig. 3b, ×5.

Figs. 4a, b. *Turbinaria frondens* (Dana, 1846)
St. 1, Tr. 11, Kabira, Ishigaki-jima.
Fig. 4a, ×1, Fig. 4b, ×5.

Figs. 5a, b. *Millepora exaesa* Forskål, 1775
St. 3, Tr. 4, Shiraho, Ishigaki-jima.
Fig. 5a, ×0.67, Fig. 5b, ×5.

Figs. 6a, b. *Millepora tenella* Ortmann, 1892
St. 2, Tr. 2, Yonehara, Ishigaki-jima.
Fig. 6a, ×0.67, Fig. 6b, ×5.

Figs. 7a, b. *Heliopora coerulea* (Pallas, 1766)
St. 1, Tr. 31, Kabira, Ishigaki-jima.
Fig. 7a, ×1, Fig. 7b, ×5.

Plate 23

Fig. 1. *Stylophora pistillata* Esper, 1797
Miyako-jima Limestone, loc. no. F108, Miyako-jima. ×3.

Fig. 2. *Acropora hyacinthus* (Dana, 1846)
Wan Formation, Kamikatetsu, Kikai-jima. ×3.

Fig. 3. *Acropora palifera* (Lamarck, 1816)
Miyako-jima Limestone, loc. no. K18, Miyako-jima. ×3.

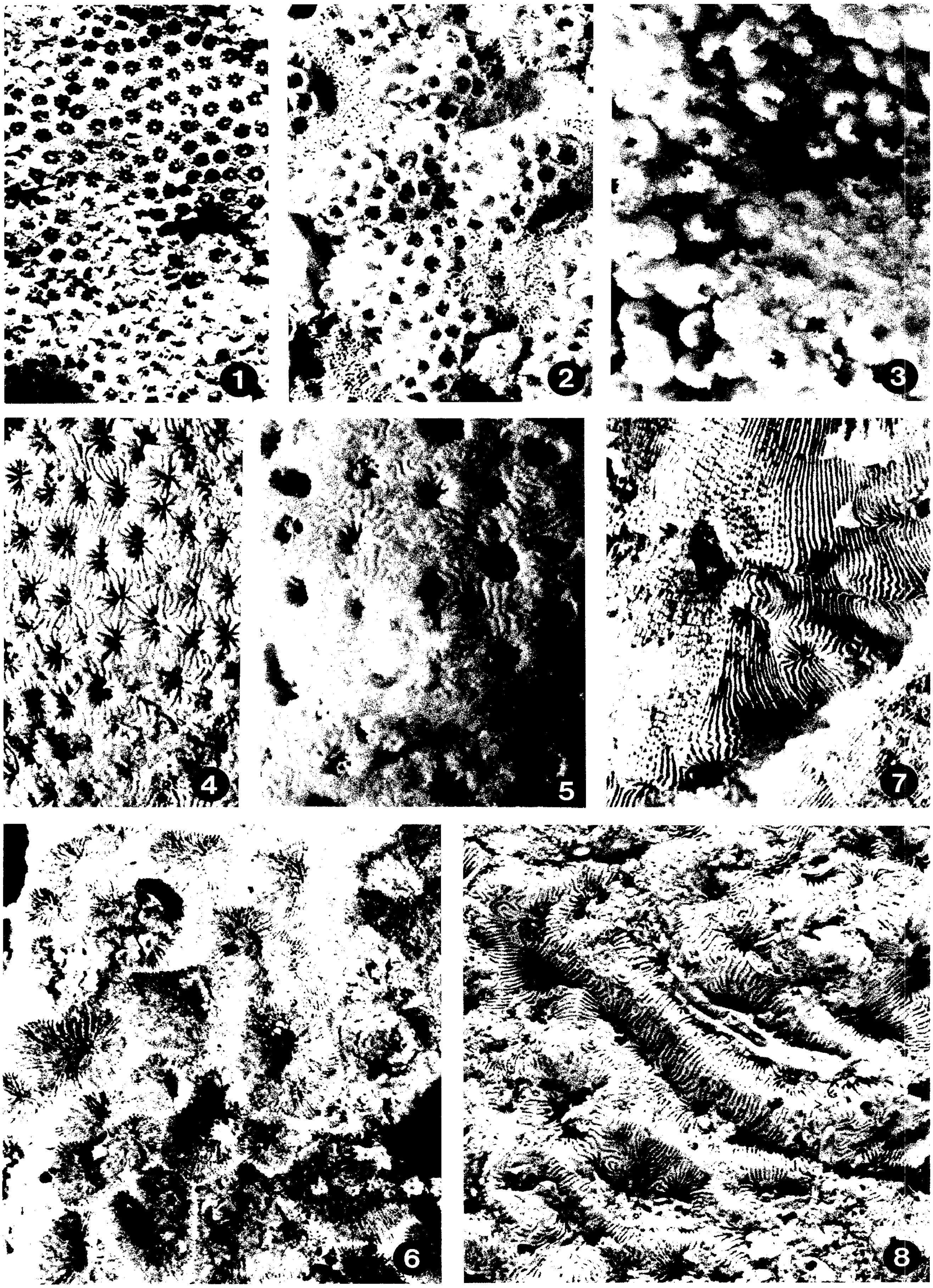
Fig. 4. *Pavona minuta* Wells, 1954
Miyako-jima Limestone, loc. no. K61, Miyako-jima. ×3.

Fig. 5. *Pavona yamanarii* (Yabe & Sugiyama, 1933)
Miyako-jima Limestone, loc. no. K50, Miyako-jima. ×3.

Fig. 6. *Gardineroseris planulata* (Dana, 1846)
Miyako-jima Limestone, loc. no. K61, Miyako-jima. ×3.

Fig. 7. *Leptoseris hawaiiensis* Vaughan, 1907
Takigawa Formation, Hyakunodai, Kikai-jima. ×3.

Fig. 8. *Leptoseris mycetoseroides* Wells, 1954
Wan Formation, Kamikatetsu, Kikai-jima. ×3.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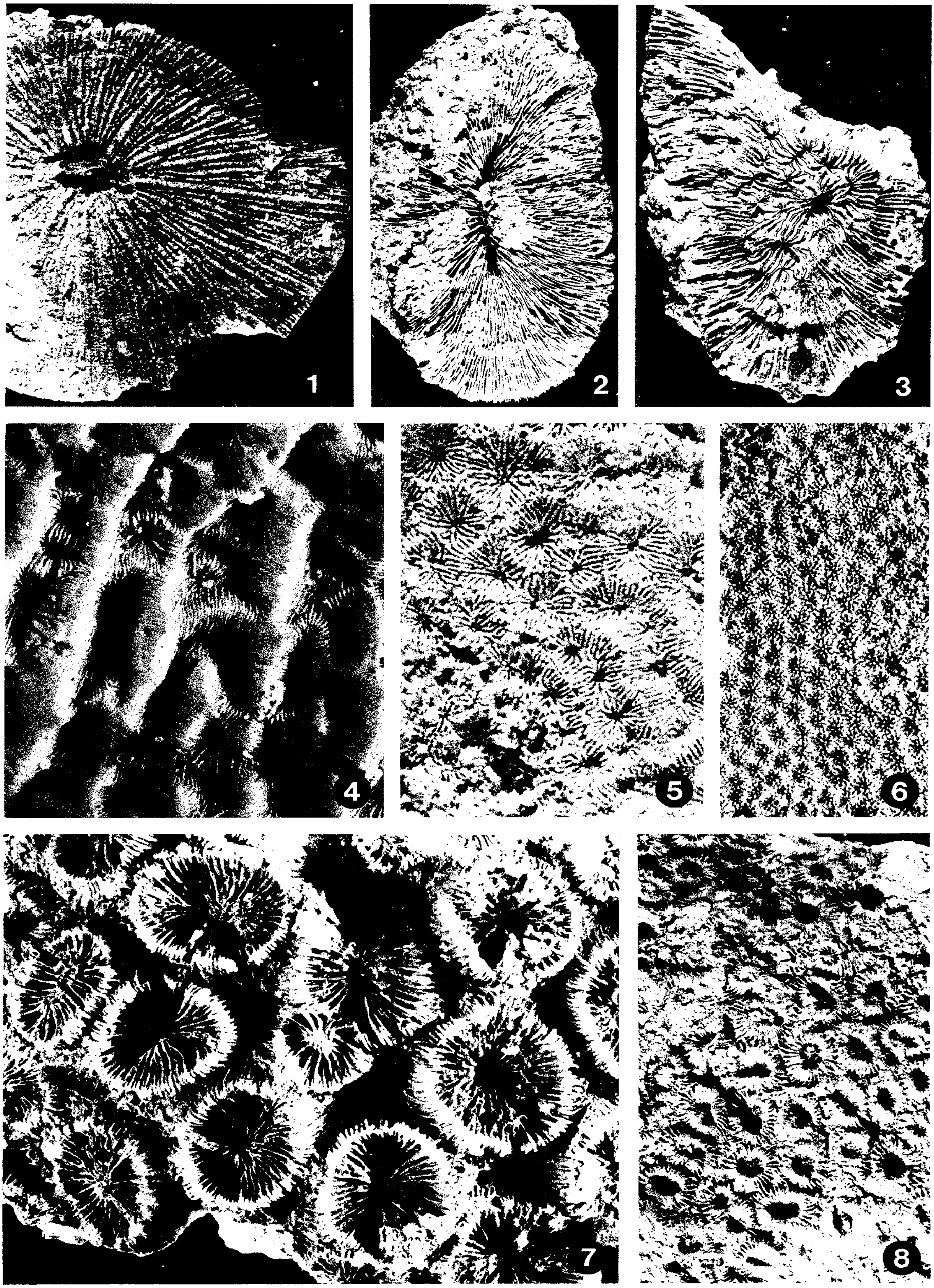
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Plate 24

Fig. 1. *Cycloseris cyclolites* (Lamarck, 1801)
Miyako-jima Limestone, loc. no. K46, Irabu-jima. ×2.

Fig. 2. *Fungia scutaria* Lamarck, 1801
Takanasaki Formation, loc. no. H1, Hateruma-jima. ×0.5.

Fig. 3. *Sandalolitha robusta* (Quelch, 1886)
Takanasaki Formation, loc. no. H7, Hateruma-jima. ×0.5.

Fig. 4. *Leptoseris yabei* (Pillai & Scheer, 1976)
Takanasaki Formation, loc. no. H1, Hateruma-jima. ×3.

Fig. 5. *Coscinaraea columna* (Dana, 1846)
Miyako-jima Limestone, loc. no. K18, Miyako-jima. ×3.

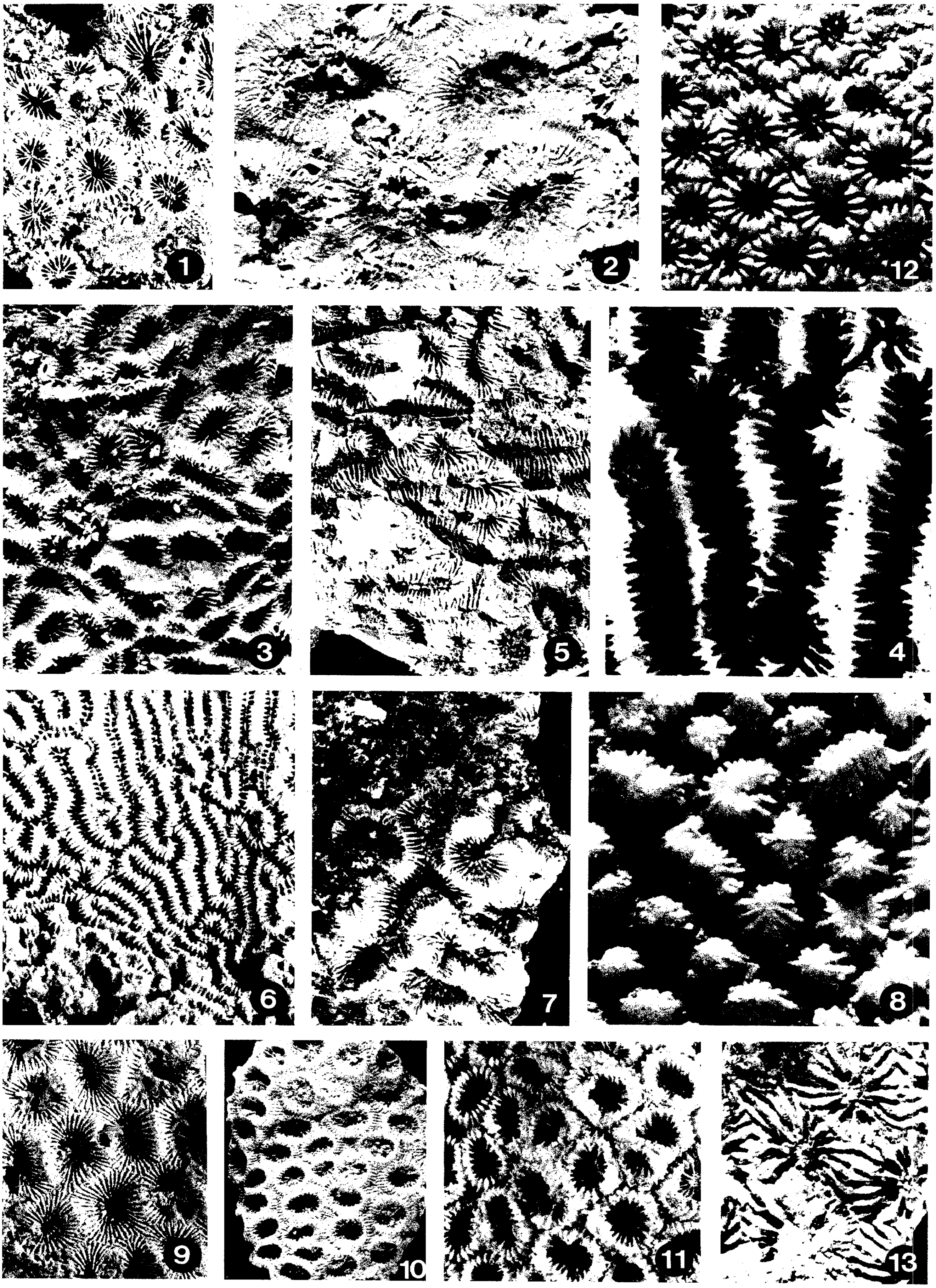
Fig. 6. *Porites* sp.
Miyako-jima Limestone, loc. no. K61, Miyako-jima. ×3.

Fig. 7. *Favia maxima* Veron, Pichon & Wijsman-Best, 1977
Miyako-jima Limestone, loc. no. K49, Miyako-jima. ×1.

Fig. 8. *Favia stelligera* (Dana, 1846)
Miyako-jima Limestone, loc. no. K51, Miyako-jima. ×1.

Plate 25

Fig. 1. *Favia pallida* (Dana, 1846)
Wan Formation, Kamikatetsu, Kikai-jima. ×1.
Fig. 2. *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977
Miyako-jima Limestone, loc. no. K55, Miyako-jima. ×1.
Fig. 3. *Goniastrea pectinata* (Ehrenberg, 1834)
Takanasaki Formation, loc. no. H1, Hateruma-jima. ×1.
Fig. 4. *Platygyra daedalea* (Ellis & Solander, 1786)
Miyako-jima Limestone, loc. no. F108, Miyako-jima. ×3.
Fig. 5. *Platygyra lamellina* (Ehrenberg, 1834)
Miyako-jima Limestone, loc. no. K20, Miyako-jima. ×1.
Fig. 6. *Leptoria phrygia* (Ellis & Solander, 1786)
Miyako-jima Limestone, loc. no. K50, Miyako-jima. ×1.
Fig. 7. *Oulophyllia crispa* (Lamarck, 1816)
Miyako-jima Limestone, loc. no. K32, Miyako-jima. ×0.67.
Fig. 8. *Hydnophora microconos* (Lamarck, 1816)
Okierabu-jima Formation, Ashikiyora, Okierabu-jima. ×3.
Fig. 9. *Favites abdita* (Ellis & Solander, 1786)
Miyako-jima Limestone, loc. no. K18, Miyako-jima. ×1.
Fig. 10. *Montastrea curta* (Dana, 1846)
Wan Formation, Kamikatetsu, Kikai-jima. ×1.
Fig. 11. *Montastrea valenciennesi* (Edwards & Haime, 1848)
Takanasaki Formation, loc. no. H1, Hateruma-jima. ×1.
Fig. 12. *Plesiastrea versipora* (Lamarck, 1816)
Miyako-jima Limestone, loc. no. K29, Miyako-jima. ×3.
Fig. 13. *Diploastrea heliopora* (Lamarck, 1816)
Miyako-jima Limestone, loc. no. K34, Miyako-jima. ×2.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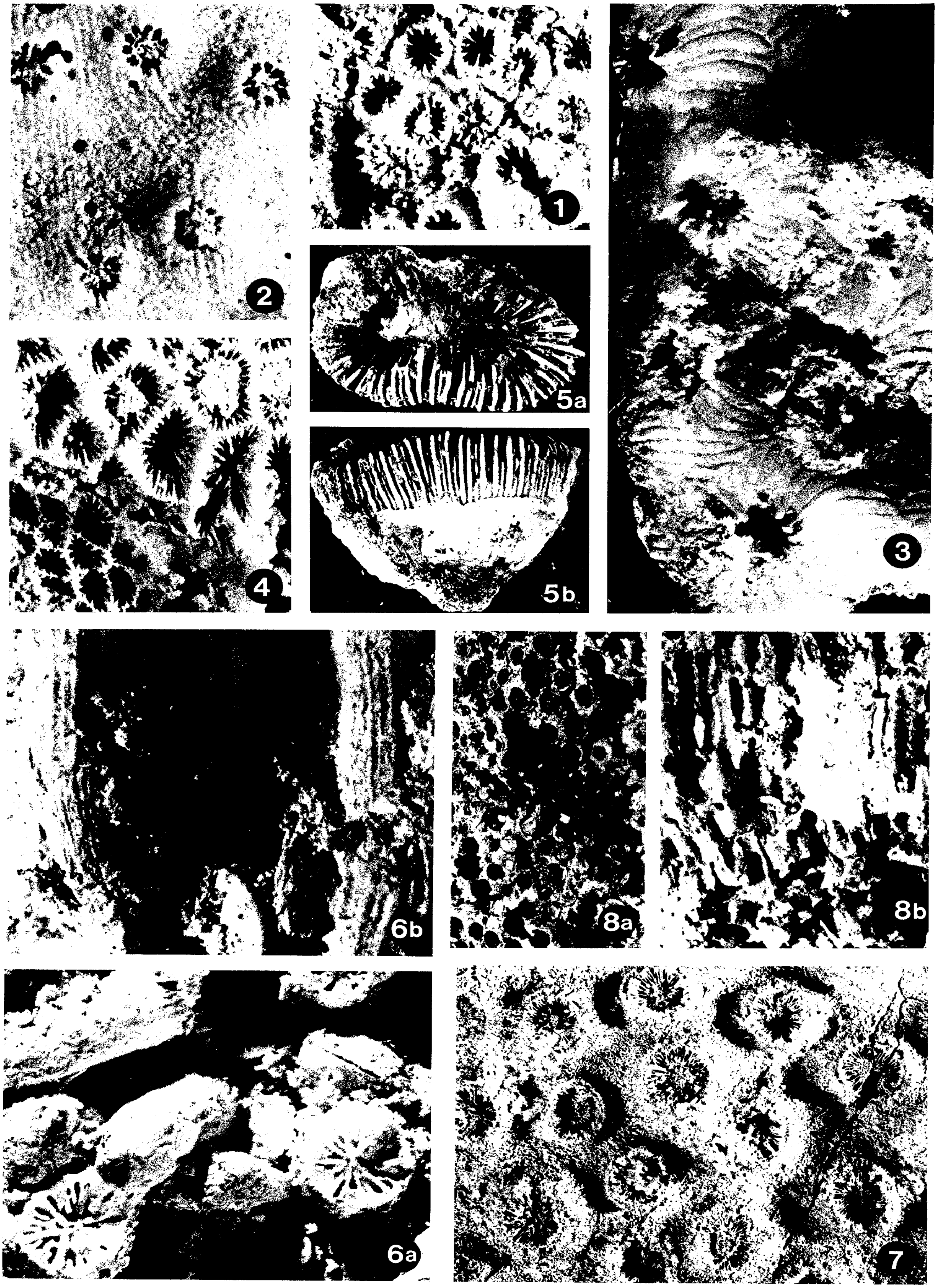
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Plate 26

Fig. 1. *Echinopora hirsutissima* Edwards & Haime, 1849
Miyako-jima Limestone, Guskube, Miyako-jima. ×2.
Fig. 2. *Echinopora lamellosa* (Esper, 1795)
Miyako-jima Limestone, loc. no. F108, Miyako-jima. ×3.
Fig. 3. *Echinopora mammiformis* (Nemenzo, 1959)
Naha Formation, Yomitan, Okinawa. ×3.
Fig. 4. *Leptastrea purpurea* (Dana, 1846)
Miyako-jima Limestone, loc. no. K29, Miyako-jima. ×3.
Figs. 5a, b. *Trachyphyllia geoffroyi* (Audouin, 1826)
Miyako-jima Limestone, loc. no. K4, Miyako-jima. ×1.
Figs. 6a, b. *Cladocora ? kabiraensis* Eguchi, 1975
Takigawa Formation, Takigawa, Kikai-jima. ×3.
Fig. 7. *Turbinaria* aff. *peltata* (Esper, 1794)
Miyako-jima Limestone, loc. no. F118, Miyako-jima. ×1.
Figs. 8a, b. *Tubipora musica* Linnaeus, 1758
Miyako-jima Limestone, loc. no. K26, Miyako-jima. ×2.

Plate 27

Fig. 1. X-radiograph of *Porites australiensis* collected from the moat (0 meter in depth) of St. 1, Kabira, Ishigaki-jima. $\times 0.95$.

Fig. 2. X-radiograph of *Porites australiensis* collected from the reef slope (13 meters in depth) of Yoan, Amami-Oshima. $\times 0.95$.

Fig. 3. X-radiograph of *Porites australiensis* collected from the reef slope (30 meters in depth) of St. 4, Sesoko-jima. $\times 0.95$.

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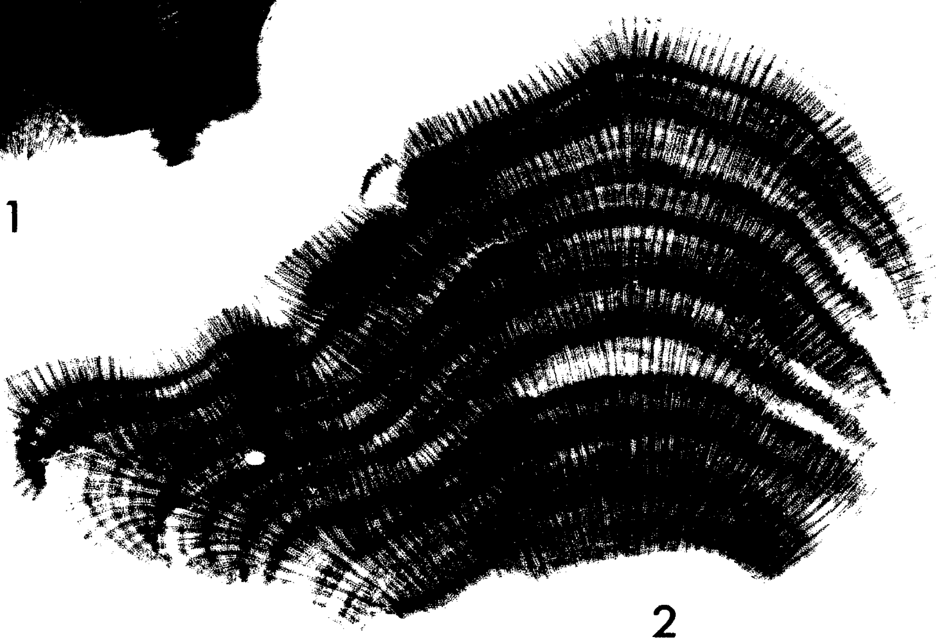

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